GROWTH, REPRODUCTION, AND UNICELLULAR ENDOSYMBIOTIC ALGA IN THE GIANT SCALLOP, *Placopecten magellanicus* (GMELIN), IN PORT AU PORT BAY, NEWFOUNDLAND

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Growth, reproduction, and unicellular endosymbiotic alga in the giant scallop, *Placopecten magellanicus* (Gmelin), in Port au Port Bay, Newfoundland

by

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Abstract

Aspects of the growth of the giant scallop, *Placopecten magellanicus* (Gmelin), in Port au Port Bay are presented. Von Bertalanffy growth equations have been fitted to selected shell dimensions of the mollusc. It was shown that there is no difference in the growth rate of male and female scallops. When growth rates of the bivalve from different beds within the bay are compared it was found that the largest and most prolific bed had the slowest growth rate. Growth differences are attributed to density-dependent and local sediment composition factors since other environmental influences within the bay are relatively uniform. Fine clay-silt was found to be a less favourable environmental substrate than larger sediments.

Age and height composition data suggest that the scallop stocks have recovered sufficiently from the overfishing during the early 1950's.

Gametogenesis and spawning are described. Histological changes accompanying the breeding cycle are also presented. Spawning is protracted, some scallops first spawning in June. This is followed by a major spawning in the fall. The spring spawning is minor and only a few individuals seem to take part.

Some aspects of a heterospecific relationship between the scallop and a unicellular endosymbiotic alga tentatively reported as a zoochlorella are presented. The association is not universal. The presence of adequate light seems to be an essential factor limiting its incidence to shallow-water

populations of the species. The effect of the alga upon the molluscan host is discussed. Present evidence indicates that the endosymbiont is a facultative parasite.

INTRODUCTION

The giant or sea scallop, *Placopecten magellanicus* (Gmelin), is a large bivalve mollusc belonging to the family Pectinidae of the order Anisomyaria. The species has been known by a wide variety of scientific names. The complete synonymy of the species exclusive of certain fossil synonyms has been traced by Merrill (1959). He attributes much of the synonymy of *P. magellanicus* to the fact that juvenile scallops were not recognized as such. The most commonly accepted name for the giant scallop today is *Placopecten magellanicus* (Gmelin).

The family Pectinidae is represented in Newfoundland by two species, the only other pectin in the area being the Icelandic scallop, *Chlamys islandicus* (Müller). In the present study only the giant scallop is considered, the word scallop being used synonymously with it.

The 'meat' or the adductor muscle of the giant scallop is widely accepted as a luxury food item. The Icelandic scallop is also considered good eating, but their smaller size and the lack of sufficient numbers of them makes their harvest scarcely profitable. The giant scallop is marketed both in Canada and the United States usually as a frozen product. Only the large adductor muscle is consumed at the present time, although the gonads or 'roe' are sometimes taken.

The giant scallop is confined to the northwest Atlantic and has a geographical range from the north shore of the Gulf of St. Lawrence to Cape Hatteras, North Carolina (Posgay, 1957). The most northerly record of capture of giant scallops was made at the northeast entrance to Pistolet

Bay, Newfoundland (Squires, 1962). They are usually found in depths ranging from about 10 to 60 fathoms. They occur in shallower water in the northern portion of their range. Verrill and Smith (1873) recorded them from Passamaquoddy Bay and Bay of Fundy in depths as shallow as one fathom. Merrill (1959) extends the bathymetric range to 210 fathoms. Where conditions are favourable, scallops frequently occur in high densities called scallop beds. Such concentrations usually support commercial fisheries. Giant scallop beds of sufficient extent and density to support commercial fisheries occur from Virginia Capes (N. Lat. 36° 50') to Port au Port Bay, Newfoundland (N. Lat. 48° 40'). In recent years giant scallops have been exploited commercially on Georges Bank, in Cape Cod Bay, Massachusetts; along the coast of Maine in the Bay of Fundy, especially off Digby, Nova Scotia; in the southern Gulf of St. Lawrence; on St. Pierre Bank and in Port au Port Bay, Newfoundland. In the centre of their range scallops have been very successful and have withstood heavy exploitation. Georges Bank, where most of the fishing effort is concentrated, is the largest producer. Most of these areas continue to be prosecuted by the fishery. Towards the extremes of their range scallops have generally been less successful and have not withstood continued heavy exploitation (Dickie and Medcof, 1963). The beds in Port au Port Bay, for example, supported a good fishery until the depletion of the stocks by over-exploitation in the early 1950's.

The definitive work on the basic biology of the giant scallop is perhaps that of Drew (1906) who described the habits, anatomy and embryology of the mollusc from Orono, Maine. Other important contributions are those of Stevenson (MS, 1932 and MS, 1936) who investigated the life history and some

environmental relationships of the mollusc; Posgay (1950, 1953, 1957, and 1963) has studied various aspects of the biology and population dynamics of the scallop in the Georges Bank area; Dickie (MS, 1951; MS, 1953; 1955, 1958) and Dickie and Medcof (1963) have made several important contributions to understanding the population dynamics of the species, including the effects of high temperature on its survival; Baird (1953) made some observations on the little known early life history of the giant scallop; the synonymy and some of the commensals of the scallop have been dealt with by Merrill (1959 and 1960); faunal associations with the giant scallop have also been investigated by Caddy and Chandler (MS, 1968) and Scott (MS, 1968). Merrill and Posgay (1964) have derived the average instantaneous natural mortality rate of scallop stocks on Georges Bank using a technique developed by Dickie (1955). The growth rates of giant scallops have been determined for the Gulf of St. Lawrence and the Bay of Fundy areas (Stevenson, 1936; Dickie, MS, 1951 and MS, 1953 and Stevenson and Dickie, 1954). Posgay (1953) has similarly determined the growth rate of scallop stocks in Cape Cod Bay. More recently Merrill *et al.* (1966) have computed the growth rate of scallops from Georges Bank and have discussed the objectivity of the several criteria normally used to identify annual rings in the scallop. They have also demonstrated that the annual rings on the surface of the shell are recorded, sometimes more clearly, on the calcareous plates of the resilium.

For an animal of such commercial importance comparatively little information has been published concerning reproduction in the giant scallop. On the basis of his work, Drew (1906) concluded that the sexes were separate and that the gametes matured at approximately the same time.

He also studied the embryology and concluded that larval development was typical of the lamellibranchs. The time of spawning has been recorded from several areas and summarized by Dickie (1955). Although attempts have been made to follow cyclic changes in the gonad through histological study (Welch, MS, 1950 and Posgay, pers. comm. 1967), there are no published records on the maturation and seasonal gonadal changes in the giant scallop. The observations of Welch were of somewhat limited scope and were designed primarily to determine the spawning period of adult scallops.

The breeding of several other pectinids including *Pecten maximus* L. in the waters off the south of the Isle of Man has, however, been investigated rather thoroughly by Fullarton (1890), Dakin (1909), Tang (1941) and more recently by Gibson (1956) and Mason (1958). The sexuality and spawning of six other pectinids in that area have also been investigated: *Chlamys opercularis* (L.) by Amirthalingam (1928) and Aravindakshan[1] (1955); *C. distorta* (Da Costa), *C. varia* (L.), *C. tigerina* (O. F. Müller), *C. striata* (O. F. Müller) and *C. furtiva* (Lovén) by Reddiah (1962).

The reproductive biology of the bay scallop, *Aequipecten irradians* (Lamarck), has similarly been well investigated (Belding, 1910; Gutsell, 1930 and Sastry, 1963, 1966, 1968).

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[1]Ph.D. Thesis, University of Liverpool, 1955 (not seen).

At the present time there are few published records concerning endosymbiotic microorganisms in the giant scallop. Stevenson (MS, 1936) found two ciliate protozoans, *Lichnophora* sp. and *Trichodina* sp. attached to scallop eggs in early stages of development. Laird (cited by Medcof and Bourne, 1962 and Dickie and Medcof, 1963) also recorded a trichodinid in fresh scallops collected near St. Andrews, New Brunswick. He (pers. comm. 1969) found this organism and *Lichnophora* sp. both abundant there. A flagellate *Hexamita* has been reported in moribund aquarium-held scallops (Medcof, 1961).

Scope of present investigation

The present study was begun because virtually nothing is known of the biology of the shallow-water northern populations and in particular of the scallop stocks in Port au Port Bay. Exploratory work and assessment of scallop populations both in inshore and offshore areas of Newfoundland have been conducted from time to time to locate potential beds of commercial promise (Dickie and Chiasson, 1955; Squires, 1962; Rowell *et al.*, MS, 1966). During the course of such exploratory work incidental observations were sometimes made on length composition, meat yields, growth rates and less frequently on the gross macroscopic state of the gonads.

This investigation explores the population structure, longevity, rate of growth, reproduction and general biology of the giant scallop in Port au Port Bay. Growth characteristics of the mollusc from three selected beds within the bay are described. An attempt is made to determine the natural mortality of the mollusc from one of these beds. The history of production and the status of the Port au Port scallop fishery, together with future possibilities are discussed.

Cyclic changes in the gonad are followed with the help of histological preparations and these are related to the reproductive cycle of the scallop within the bay.

During the course of investigations on the biology of the giant scallop on the west coast of Newfoundland it was observed that the mantle tissue of the mollusc was often coloured green. On closer examination it was found that the green colour was due to the presence of a symbiotic[2] unicellular alga on and within the tissues containing them. The alga is tentatively reported as a zoochlorella. It is suggested that there is an inverse relationship between the degree of infection and the condition of the host, also that the relationship is parasitic.

Although comparisons are sometimes made with other areas the study deals almost exclusively with the Port au Port area.

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[2]As has been shown later, the author recognizes that the association here is one of facultative parasitism. The term symbiosis is used throughout this paper to designate a heterospecific association as was originally proposed by De Bary (1879) and formally accepted by the Commission on Terminology designated by the American Society of Parasitology in 1933 (J. Parasitol., p. 326-329, 1937). More recently several workers including Henry (1966), Rees (1967) and Cheng (1967) have re-emphasized the importance of the broadness of this ecological term in an attempt to exclude erroneous connotations of necessary mutualism.

Distribution of scallop beds in Newfoundland

Exploratory fishing in Newfoundland coastal waters in 1957 and 1958 revealed several large beds of giant scallops on the west coast and smaller and fewer beds on the southwest coast (Squires, 1962).

Fair-sized coastal populations of scallops were found in (a) Port au Port Bay, (b) Bay of Islands area, (c) Bonne Bay, (d) Port Saunders area and (e) in the vicinity of St. John Bay on the west coast of Newfoundland.

Scallop beds of moderate size were located in St. Mary's, Placentia and Fortune Bays on the southeast coast of the island (Fig. 1).

General description of the study environment

The coastal areas of western Newfoundland are distinguished by two major physiographic features, coastal lowlands and cliffed-shore highlands. Throughout the western shoreline the waters seldom exceed 30 fathoms within 10 miles of the coast. The waters are much deeper in the fiords or near their heads.

One of the principal agents of erosion in western Newfoundland was glacial ice. Evidence of Pleistocene glaciation is well exemplified by the presence of fiords such as those in the Bay of Islands and Bonne Bay. Frequently the ice left the hills bare of residual soils and clays depositing this material upon the submarine shelf. The present distribution of sediments on the shelf is thought to be the result of either the submarine erosion of glacial deposits or the erosion of the glacially-modified landscape (Lilly, MS, 1965). The erosional processes have affected the distribution of bottom fauna on the coastal marine shelves.

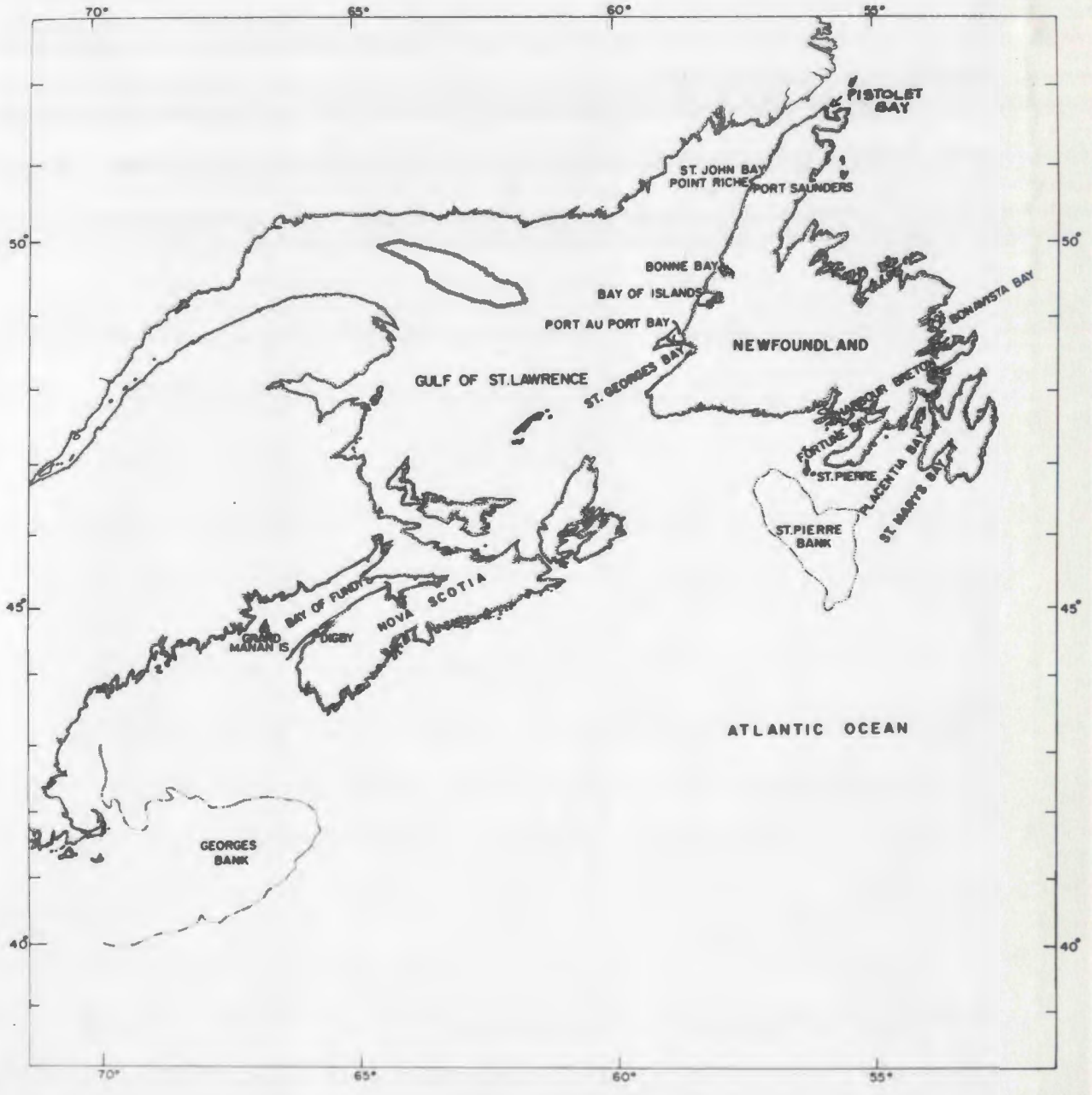


Fig. 1. Place names mentioned in text.

The Port au Port Bay environment

The bottom of Port au Port Bay is composed of a variety of sediments ranging from fine, anaerobic muds to coarse talus. The sediment grain sizes found in the bay depend primarily on the velocity of the transporting current in the bottom waters (Mr. Jim Shears, pers. comm. 1966).

Much of the coastal sands and finer gravels often found on scallop beds are of glacial origin refurbished now by attrition of the present shoreline. In general the finer grained sediments (silts and muds) are confined to the deeper parts of the bay, where tidal currents are weak or non-existent and where wave action has little effect. Shallow-water depressions with restricted water circulation may also be characterised by fine sediments.

Lilly found that the most prolific scallop beds occurred where the muds give rise shore-wards to finer gravels and silts. The shellfish is also found in ledges in the bedrock.

Arrangement and description of scallop beds in Port au Port Bay

While scallops are generally found in shallow water close to the shore throughout the length of the shoreline, the best concentrations are found in four major beds within the bay (Fig. 2). These are the (a) West Road bed, (b) Piccadilly bed, (c) Fox Island River bed and (d) Boswarlos bed.

The following descriptions are based on the diving observations of the late Hugh Lilly (MS, 1965) together with supplemental information gathered during the present investigation.

(a) West Bay bed (West Road bed)

This bed extends from one mile of north of Piccadilly to the base of Long Point. The bed is bounded on the north by muds and on the south by mixed silt, sand and gravel. It averages approximately 0.3 miles in width and is about 6 miles long. The bed is located in depths ranging from 4 to 7 fathoms.

(b) Piccadilly bed

The Piccadilly bed is the smallest bed in the bay. It is about 4 miles long and located in 4-5 fathoms of water. Lilly reported numerous young scallops on this bed and noted that larger scallops were relatively scarce.

(c) Fox Island River bed (Fox Island Channel or Fox Island bed)

This is a large discontinuous bed, the major separation occurring west of Two Gut Barachois by a wide stretch of sand. It is thought that heavy land drainage into the area may be responsible for its absence there. The more southerly bed is often referred to as the East Road bed. The total length of both beds is about 14 miles. The largest concentrations of scallops occur in mixed silty organic mud located in about 10-16 fathoms in the north and between 6-9 fathoms in the south.

Scallops on this bed are reported to be generally concentrated in a narrow band more or less parallel to the coast and found farthest from the shoreline on the east side of the bed. Lilly reported densities as high as 17 scallops in a 20-ft square of bottom in 15 fathoms of water.

(d) Boswarlos bed

The Boswarlos bed is about 4 miles long and averages about 0.5 miles wide. The bed is bounded on the north by the 11-fathom contour and in the south by the 5-fathom contour. The bottom consists chiefly of sand and gravel toward the shore with sand and silt mixed with mud toward the 11-fathom contour. The smooth sand and gravel bottom is sometimes interspersed by ledges and large rocks.

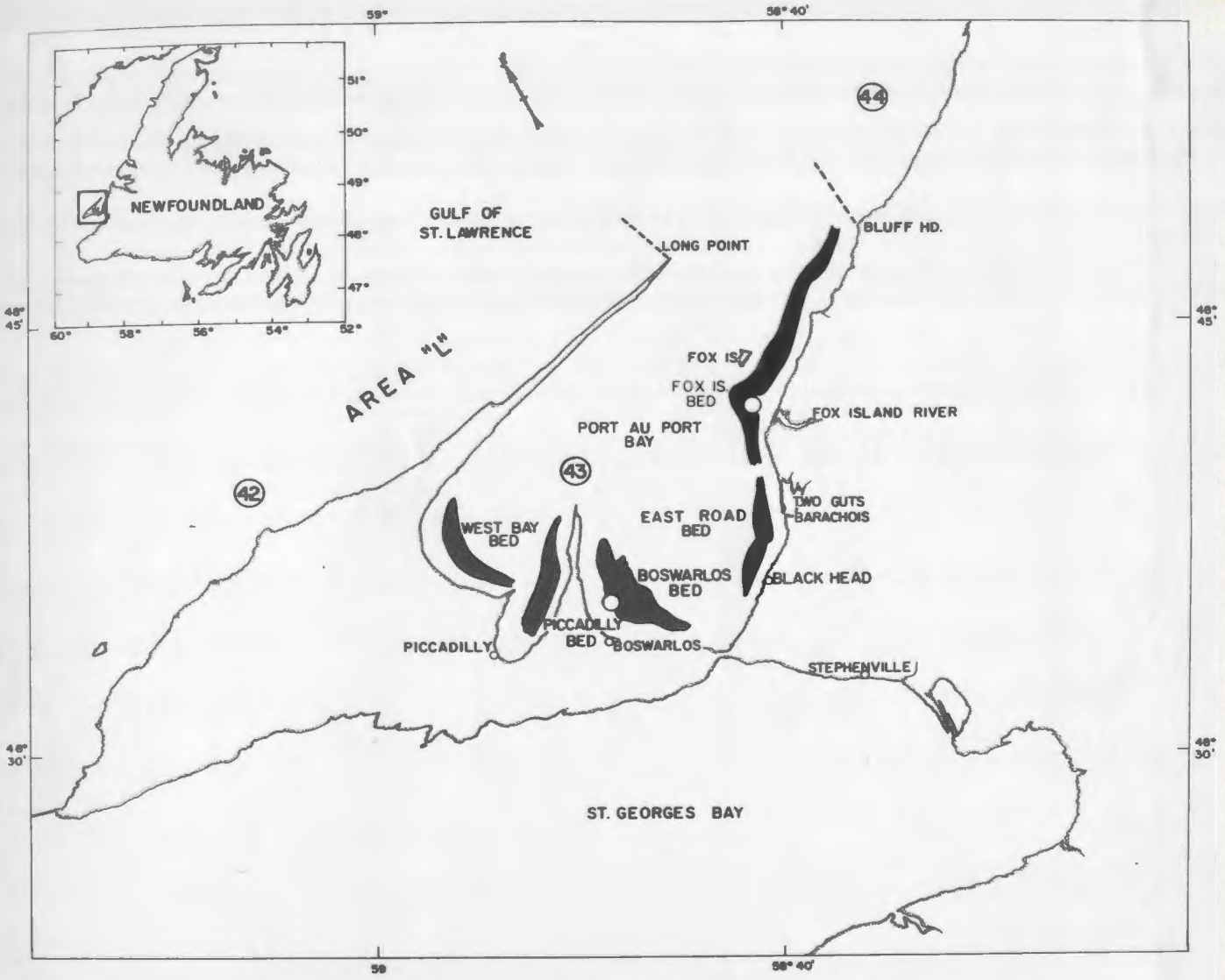


Fig. 2. Distribution of scallop beds in Port au Port Bay, Newfoundland. Approximate positions of density surveys conducted on the Boswarlos and Fox Island River beds are circled.

Several other areas with isolated patches of scallops have been reported from the bay. The concentrations of scallops vary widely within the major beds. Anomalously high concentrations occur from place to place.

History of production in the Port au Port area

The following history has been compiled from the Canada Department of Fisheries statistics together with verbal reports by fishermen.

The Newfoundland fishery has always been an inshore operation, fishing centred in Bay of Islands, Port au Port, St. Mary's, Placentia and Fortune Bays. Scallops were probably first fished in Newfoundland in the Fortune Bay area in 1935 (Thompson, 1936).

Scallops have been known to occur in Port au Port Bay for many years before they were exploited commercially. According to fishermen's reports dragging in the area has gone on for a longer time than is documented in official records. Before 1936, the beds were fished casually by amateurs for their own domestic requirements. At about 1936 a fishery for scallops and clams began as a side line of the well established lobster canning industry at Piccadilly in Port au Port Bay (Fig. 2). First attempts to market fresh frozen scallops were begun in the same year. Since then a small number of small boat operators drag for scallops within the bay each year immediately following the lobster fishing season. Newfoundland fishery regulations (Subsection (1) of section 32) prohibit scalloping within the bay during the lobster fishing season which lasts from April 20 to July 5. The catches are therefore not evenly distributed throughout the year and the effort is concentrated largely on the Fox Island River and West Bay beds (Fig. 2). When scallops are relatively abundant, increased landings are made usually by larger and better equipped boats from Maritime ports. As the catches decline the outside boats leave the area and fishing is carried on by small boats owned and operated locally.

The statistical history of the fishery up to the mid-1950's has been reviewed by Squires (1962). Table 1 shows the landings of scallops in Newfoundland for the period 1952-68. Column 2 gives the total Newfoundland landings during each year in all areas. Column 3 shows the landings in Subarea L as reported by the Canada Department of Fisheries statistics which includes two statistical sections showing areas in which scallops are exploited commercially. Examination of the records at the Federal Department of Fisheries in St. John's, however, permitted a limited breakdown of the landings and of the effort expended in each of these two areas during the period 1958-60 and again from 1965 to 1967 inclusive. These are tabulated in columns 4 and 5.

Moderate catches were made from about 1946 to 1953 (Squires, 1962). Encouraged by the success of the local industry, Nova Scotian scallopers appeared on the bay first in 1951 and again in 1954 and 1955. The quantities of scallops taken from the bay during the years 1950-55 were high for the size of the bay. A peak was reached in 1954 when the catch yielded 415,000 lb of meats. In 1955 the landings were still appreciable reaching 369,000 lb of which 343,000 lb were caught by Nova Scotian scallopers. The slow moving local industry was obviously affected by the large catches and the total local landing in 1955 was reduced to 26,000 lb. In the following year the combined total taken from the bay dropped to 16,000 lb. Thus the scallop landings in Port au Port Bay increased from the beginnings of the fishery in the late 1930's with minor fluctuations and reached a peak in 1955, after which a spectacular drop in the population or availability occurred. Much of the fluctuations exhibited

during the more or less stable period may be due to minor fluctuations in abundance.

The landings over the years suggest that under the conditions prevailing during the period 1946-55, the best sustained catches were made when landings averaged around 80,000-100,000 lb. This may, however, be a fortuitous result of concurrent changes in population levels or in the intensity of fishing. But that a fluctuation of considerable amplitude was responsible for the diminished catches in the late fifties is unlikely. However, in the absence of figures upon the magnitude of natural fluctuations and in particular without reliable estimates of the yearly effort expended during the period it is not possible to derive the optimum intensity of fishing for the area.

The accuracy of the figures reported is uncertain. Local sales still go unreported and it is probably a fact that published figures are somewhat under the true values. In 1966, for example, total landings in the bay as gathered by weekly collection of catch records reached over 7000 lb of which only 5300 lb is reported in the statistics compiled by the Department of Fisheries. The estimate of effort as measured by the number of rakes operating in the area does not appear to be reliably reported. Again in 1966, 41 rakes are reported to have been in operation in the Port au Port area. This figure although somewhat consistent with those of previous years is at least 4 times the true figure. To the best of the author's knowledge, there were in fact only 9 scallopers in the bay that year each with a single hand drag. The Port au Port Fishermen's Producers Cooperative operated a longliner specially rigged for scallop dragging. Of the ten boats, five were fishing on the Fox Island River bed (Fig. 2). The

fishermen deliberately refrained from scallop fishing in 1966 because there was no ready market for the meats. The few who did operate sold scallop meats as cheaply as thirty cents a pound. In 1968 scallops were fetching sixty to ninety cents per lb and consequently landings have again gone up. Most of the landings reported for 1968 is reported to have come from Port au Port Bay (pers. comm. Mr. Dunne 1967, Federal Department of Fisheries). Thus economic factors have also influenced the course of the fishery.

While the total catch is a useful index, economically it has little biological significance unless the effort expended in catching the shellfish and types of gear are constant. Neither of these appears to have been constant in the scallop fishery of Port au Port Bay. There is no estimate of the time expended by the fishery. It is likely that at various periods, depending on varying economic incentives, the time expended in fishing by each man or boat has varied widely.

Such statistics as exist on the scallop fishery in Port au Port Bay suggest that overfishing was the major contributing factor to the decline in catches. In particular the high fishing mortality during 1954 and 1955 contributed substantially to stock depletion and accounts for the 1956-58 sharp drop in landings. This does not exclude the possible operation of biological factors. Fluctuations in abundance are characteristic of scallop populations and have been well documented in the giant scallop (Dickie, 1955). There is no evidence to suggest that the low catch in 1956 was the result of a mass mortality operating within the bay the previous

year. It is therefore reasonable to assume that natural mortality in 1955 was not quite sufficient to reduce the catches by the amounts indicated. A third possibility, that of migration, may also be discounted. Although scallops can swim, their swimming powers are limited and little or no migration of adults has been shown through tagging, growth studies and general observations (Dickie, 1955; Baird, 1958; Posgay, 1963).

Present-day fishing methods in the bay are outmoded and inefficient and dragging is largely carried on by small lobster fishing type of boats. Many of the local operators continue to fish the same grounds every year and are reluctant to move into new areas where fishing may be more profitable.

MATERIALS AND METHODS

Sampling procedure

Samples of scallops were collected from three stations within Port au Port Bay, *viz*. (1) Boswarlos bed, (2) West Bay bed and (3) Fox Island River bed (Fig. 2).

Collections were made weekly from the Boswarlos bed during the period May-November 1966 and monthly for the same period in 1967. One

Table 1. Annual landings of giant scallop meats from the Newfoundland area 1952-68 (from Canada Dept. of Fisheries statistics and the archives of the Dept. of Fisheries in St. John's).

1	2	3	4	5	6	7	8				9
Year	Newfoundland total	Port au Port and Bay of Is. area (Subarea L)	Subarea L		Nova Scotia landings taken from Port au Port Bay	Total catch from Port au Port Bay and Bay of Islands	Number of rakes used				Landings in other Newfoundland areas
			Section 43[a]	Section 44[b]			Port au Port Bay and Bay of Islands area	Port au Port Bay	Bay of Islands	St. Georges Bay	
1952	148,000										nil
1953	179,000										nil
1954	239,000	193,900			220,700	414,700	-	-	-	-	nil
1955	49,000	26,000	-	-	342,700	368,700	-	-	-	-	nil
1956	15,000	11,000	-	-	4,800	15,800	74	-	-	-	4,000
1957	40,000	no landings	-		no landings	no landings	68	-	-	-	36,000
1958	63,000	26,400	20,600	5,800	-	as in column 3	83	-	-	-	41,000
1959	56,000	56,000	31,000	25,000	-	"	120	42 + 10[d]	68	nil	nil
1960	24,000	24,000	16,000	8,000	-	"	126	46 + 12[d]	68	nil	nil
1961	6,000	6,000	-	-	-	"	107	33	74	nil	nil
1962	20,000	20,000	-	-	-	"	111	37	74	nil	nil
1963	26,000	26,500	-	-	-	"	115	44	71	nil	nil
1964	194,000	20,300	-	-	-	"	114	43	71	4	173,000[e]
1965	58,000	15,400	6,400	8,900	-	"	110	44	66	4	41,330[e]
1966	7,800	7,800	5,300	2,500	-	"	94	41	53	4	nil
1967	49,600	800	nil	800	-	"	86	35	51	4	48,500[e]
1968	89,800[c]	-	-	-	-	"	-	-	-	-	-

[a]From Long Point to Bluff Head.

[b]From Bluff Head to Cape St. Gregory.

[c]Tentative figure up to October 1968.

- Figures not available.

[d]Rakes used west of Long Point.

[e]Refers usually to scallops landed at Harbour Breton by Maritime vessels fishing on St. Pierre Banks.

additional commercial sample consisting of 742 scallops was examined in 1968. All scallops examined from the Boswarlos bed during 1966 and 1967 were caught with a simple hand dredge. The bag, 22½ inches deep with a gape of 5 3/4 inches, carried a belly of rings with an internal diameter of 2½ inches. Adjacent rings were connected with each other by compressed circular metallic washers. The cross-bar was 3 ft long and carried teeth, 3½ inches apart, which protruded 1½ inches from the bar. The inside of the drag was covered with a small-meshed codend so as to retain small scallops. Most hauls were of 10-minute duration (effective fishing time). The dredge was towed from a 17-ft motor-boat with a 17 horse-power engine. The 1968 Boswarlos sample and the West Bay and Fox Island River samples collected in 1966 represent commercial catches by local fishermen. Instruction had been given to the fishermen to provide representative samples. Sampling areas and place names are shown in Fig. 1 and 2.

Additional samples were obtained with SCUBA from St. Mary's and Bonavista Bays on January 28 and November 23, 1967, respectively. A small number of scallops from the Georges Bank area was also examined for some aspects of this investigation. These moderately deep-water specimens were collected with a beam trawl on March 23, 1967 by the Fisheries Research Board trawler, *A. T. Cameron*. A total of 5288 scallops was examined from all areas. In addition to this, several small samples were observed during the late winter months to determine the time of formation of growth annuli.

All observations were made on live, freshly caught scallops except for the sample from Bonavista Bay, which was temporarily stored in 10% formaldehyde during transit to St. John's.

Studies on the growth and reproductive biology of the scallop are largely based on the scallop populations in Port au Port Bay. Growth curves for scallops from other areas including Digby and Georges Bank are also constructed and compared with that from the Boswarlos bed in Port au Port Bay.

Tagging

A sample of 250 scallops from the Boswarlos bed was tagged and released on August 2, 1966 in an attempt to validate the annular nature of the rings on the surface of the shell. A hole was drilled on the ear of the upper valve just over the byssal notch with Rotadent precision dental burrs (Dentalborrfabriken A-B, MALMÖ, SWEDEN). Small numbered plastic discs were then attached by means of a nickel wire. Tagged scallops were immediately returned to the bed.

Density surveys

Underwater observations by SCUBA were made to determine the density and pattern of distribution on the Boswarlos and Fox Island River beds. Approximate positions of these surveys are indicated in Fig. 2. A metal grid, one meter square, was painted white to improve its underwater visibility. This was attached to a yellow nylon rope and thrown overboard at random positions over the bed. A sufficient length of rope was allowed to run out to ensure that the grid came to rest on the sea bottom. A diver would then locate the grid underwater by following the length of the rope and without displacing it from fallen position, count and collect the scallops within the area enclosed by the grid. Immediately upon surfacing, the diver would report his count and dump the scallops onboard.

Each collection was examined for cluckers and the left valve of each live specimen was retained for ageing. This was repeated for 31 dives on the Boswarlos bed and 16 dives on the Fox Island River bed.

Field measurements

The following data were recorded in the field for each scallop examined: shell-height (the distance from the umbo to the ventral edge of the shell), body weight, weight of the posterior adductor muscle, gonad weight and wet shell weight of both valves. The condition of the posterior adductor muscle was noted and the number of annual rings was recorded whenever possible. All shells were numbered by scratching on the nacreous layer and were retained for further morphometric measurements.

Daily meteorological records were maintained throughout the study period in 1966. Air temperature, shore water temperature, surface and bottom water temperatures on the scallop beds were recorded. The bottom water temperature was obtained with a fisherman's reversing thermometer. Wind direction and sea condition were also noted. In 1967 and 1968, these observations were made only during sampling time.

Natural mortality

The natural mortality of the scallop is estimated using the method proposed by Dickie (1955). The accuracy of his method is dependent, among other things, on the accuracy of estimating the number of days paired valves, called "clappers" or "cluckers", persist after the death of the scallop.

In order to determine the natural mortality, records were kept of clucker-living scallop relationships for all samples taken in 1966. To

increase the reliability of the estimate the average time required for separation of the valves on the Boswarlos bed was determined. A sample of 96 scallops was killed on July 25 by prolonged air exposure of the animals. The dead scallops were placed in two retrievable wooden boxes lined with chicken wire so as to allow free passage of water and returned to the bed. The decaying soft parts of the scallop were carefully removed from within the valves the following day without in any way injuring the hinge line or resilium. The cluckers were then replaced in the boxes and returned to the sea bottom and re-examined weekly for valve separation. The time required for 50% of the cluckers to separate is used in the estimation of the natural mortality for the Boswarlos bed.

The natural mortalities of scallops on the West Bay and Fox Island River beds were not estimated.

Laboratory measurements

The thickness of the shell (not the valves) was determined with a deep throat micrometer caliper (L. S. Starrett Co., Athol, Mass., U.S.A.). The height of the left valve after separation was remeasured and errors of observation due to parallax were corrected. The distance from the umbo to the ventral edge was measured along the curvature of the shell. The anterior-posterior axis and the wing base were also measured (Fig. 3A).

Determination of adductor muscle scar area

The scar areas of the posterior adductor muscle were determined for samples of both right and left valves using an OTT-compensating polar planimeter with a fixed tracer arm. The accuracy of the instrument was first checked with a calibrated control ruler supplied with the planimeter.

As the device may only be used for the measurement of level areas, the outline of the scars on the shells had to be traced onto Agawan onion skin sheets before area determinations could be made. In practice, it was found necessary to guide a pointed marking device lightly along the circumference of the scar on the shell before it could be transferred onto the onion skin. Felt-tipped marking pens (0200 SCRIPTIP 39, U.S.A.) proved to be quite satisfactory for the purpose. The felt-tips became blunt with use and it was found necessary to discard used pens after about 100-150 tracings. A mean of at least two tracings was obtained for each shell. For very small scallops (less than 30 mm) and for scallops with relatively irregular or ill-defined boundaries, a mean of several determinations was used in all computations.

Age determination

Age determinations were made from the annual rings on the surface of wet left valves. Where this was impossible, as when the rings were obliterated by heavy surface growth of saxicolous crustose corallines, the calcareous parts of the resilia were used. In my examination of resilia, I found them of use only when over III^{+} years. Small resilia were firmly attached, difficult to remove and could not be read with any confidence. As the rings on the resilia were often crowded, especially towards the ventral edge of the ligament, it was found useful to immerse detached ligaments in tap water for about 4-5 hrs. This treatment caused the ligament to swell, thereby expanding the inter-annular spaces, thus showing up the growth rings more clearly. As it was possible to soak only a few ligaments

at a time, the structures were X-rayed and permanent radiographs of the ligament in the expanded state were obtained. Unless otherwise stated, all age determinations were made by the author.

Measurement of shell annuli

Growth is estimated from measurement of distances between the umbo and the annuli on the left valve. Unlike the study of fish growth, it is not necessary to convert one measurement to another (e.g. scale to fish length) for the shell-height at any age is permanently recorded on the surface of the shell and growth to successive annuli may be obtained directly by simple measurement. In previous studies, growth rates of the giant scallop have been computed by measuring the tangential distance from the umbo to the several annuli (Fig. 3B). These distances were usually measured with a pair of dividers or with a vernier caliper. In the present study the dorso-ventral distance was measured along the curvature of the shell using thin paper strips (Fig. 3C). The positions of the growth annuli on the left valve were marked off on strips of paper stretched tightly over the contour of the shell. The strips were then laid over a ruler calibrated in millimeters and the distances to the annuli read off. For purposes of comparison, a sample of 416 scallops was also measured to yield dorso-ventral heights along a straight line tangential to the curvature of the shell.

Estimation of growth

Von Bertalanffy (1938) growth curves, of the type shown in equation 1, have been fitted to four dimensional shell characters of the left valve in order to study the growth of these shell dimensions with age.

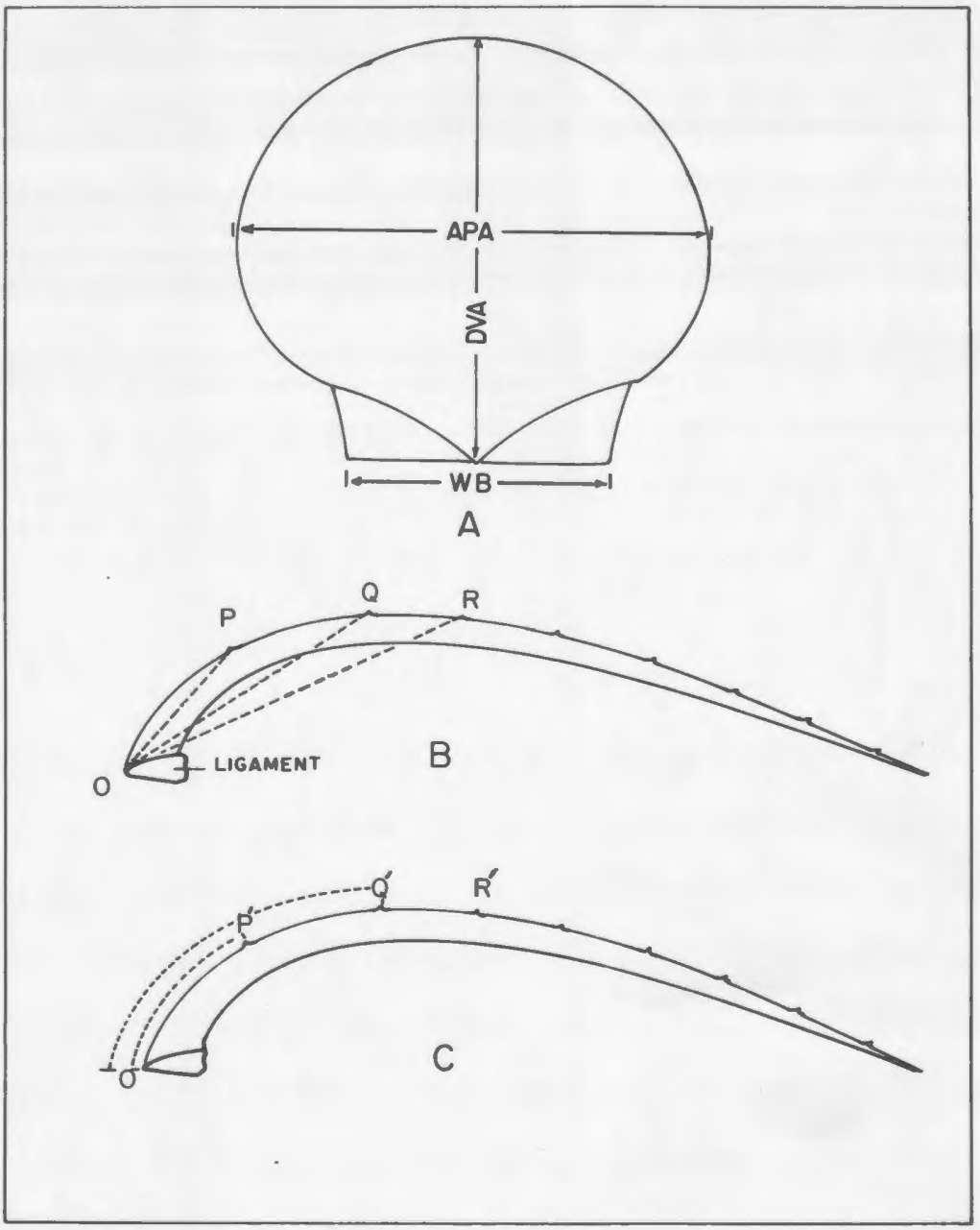


Fig. 3. Diagrammatic representation of the left valve of the giant scallop illustrating shell dimensions used in the present study:

A. Anterior-posterior axis (APA), total shell-height (DVA) and wing base (WB)

B. Tangential dorso-ventral shell-heights to annuli (OP, OQ, etc.)

C. Dorso-ventral shell-heights along curvature to annuli (OP', OQ', etc.).

Shells with distorted valves were not used in growth studies. Two methods have been employed for fitting the growth curves. The method described by

$$l_t = L_\infty [1-e^{-K(t-to)}] \quad \ldots\ldots\ldots\ldots \quad (1)$$

where L_∞ represents the average asymtotic shell dimension that a sample of the population would attain under specified conditions

K expresses the relative rate of approach to L_∞

and to is the theoretical age at zero shell dimension and is merely a scale constant.

Allen (1966a) was used for all the Port au Port Bay data. This method uses weighted averages at age for the fit. The second method is that of Lal (cited by Naidu, MS, 1966) and uses the mean of a variate at age. Both methods employ an iterative least squares procedure. The second method provided a means of extracting comparable figures for the Digby, Bay of Fundy and Georges Bank areas. The von Bertalanffy growth equations were computed on IBM 1620 at the Memorial University of Newfoundland.

Sex and maturity

All specimens collected from Port au Port Bay were examined for sex and maturity. The study of the breeding cycle was attempted in four ways. Attempts to maintain and observe spawning activity in aquarium-held scallops were in general unsuccessful and not discussed here.

A. Macroscopic and histological examination of the gonads

All gonads were examined macroscopically and microscopically at regular intervals throughout the period of study (May to November) for two

successive years (1966 and 1967). Approximately 3000 scallops of all ages were examined and classified as regards degree of development. Representative labelled gonads at each stage of development were fixed in alcoholic Bouin's solution for about 36 hrs and stored in 70% ethyl alcohol for later histological examination. Ripe or full gonads were allowed to remain in the fixative for a further 12 hrs. A series of razor-blade incisions was made on the larger gonads (over 50 mm) to facilitate uniform and complete fixation. The tissues were dehydrated and embedded in paraffin. Sections were cut of the various stages at 4.0-8.0μ, depending on the size of the gonad, and stained with Masson's trichrome or in Heidenhain's iron-alum hematoxylin followed by eosin as a counterstain. Masson's trichrome was found to be most satisfactory for the purpose.

B. Examination of smears

Gross dissections of the gonad and smears of its contents were examined regularly but more frequently during the peak of spawning for degree of motility of the sperm in the male and shape and size of ova in females. The granular nature of the deutoplasm or yolk was also noted in ripe females.

C. Plankton tows

Midwater tows were made daily during the study period in 1966 from July to October with a 24 mesh/cm plankton net. Except when prevented by inclement weather, tows were made between 9-10 a.m. (E.S.T.).

D. Collection of juvenile scallops

Attempts were also made to collect small recently settled scallops from the beds. Suitable substrates such as frayed rope ends, wooden

buoys and scallop shells were used as spat collectors. These were introduced and maintained at different depths and re-examined at regular intervals for the presence of small, recently-settled scallops.

Endosymbiotic alga

A systematic macroscopic examination of the soft parts of naturally infected scallops was conducted in the field. Records were kept of the site, frequency and intensity of infection for scallops collected from four widely separated areas: (a) Port au Port, (b) St. Mary's and (c) Bonavista Bays, Nfld., (d) Georges Bank. The scallops were arbitrarily allotted to one of four categories: uninfected, light, moderate, heavy, according to the degree of infection. Using the same criteria, the relative abundance of the organism in the mantle, gonad and bases of the posterior adductor muscle of individual scallops was also assessed.

The soft parts of several animals were fixed in Bouin's solution for histological study. Frozen cryostat sections were also examined. Masson's trichrome and Alcian blue chlorantine red were used in the histochemical study. Photomicrographs were obtained of both frozen and fixed tissues.

Most of the observations are based on scallops obtained from Port au Port Bay. A detailed study was conducted on the three major beds in this bay to investigate the effect of depth on the symbiotic association. Of the 3275 scallops examined, 2962 were from the Boswarlos bed (Fig. 2).

The results of a minor tagging program are used in this section of the paper to support the proposed mechanism by which scallops may become infected in their natural environment.

Isolation of the alga

Live infected scallops were air-freighted from Port au Port Bay and maintained in recovery tanks in running sea water for a week. The organism was isolated from a 10-year-old female.

Standard agar, stab and petri dish methods were employed. The medium consisted of sterile sea water Erd-Schreiber in 1.5% agar (Fϕyn, 1934). After repeated rinsing of the mantle tissues of the scallop in sterile sea water, algal colonies were carefully dissected out and inoculated onto the medium. A single specimen was used to initiate all the cultures.

Cultures were incubated at a temperature of 15.0 ± 0.5°C in a Psycrotherm controlled environment incubator (New Brunswick Sci. Corp.) under artificial illumination from white fluorescent tubes of 2000 lux intensity adjusted to an 18 light-hour period (Westinghouse, cool white . High output . F24T12/CW/HO).

Of the initial isolates, slants were most successful. From a total of 25 original cultures, only 5 showed positive growth after 5 weeks incubation. From two of the slant cultures a further series of ten slants were set up maintaining the same sterile culture conditions. All cultures were bacterized, the bacteria including a number of flagellated forms.

By three weeks, growth of the subcultures was good. Five further subcultures were made from these, by transferring a small suspension of cells to sterile, liquid Erd-Schreiber medium and agitating violently. The liquid cultures were then incubated under the same conditions as the agar ones.

Two cultures (one of the first slope subcultures and one of the liquid subcultures) were sent to the Department of Botany, University of British Columbia, Vancouver, where further studies are being conducted by Dr. J. R. Stein.

Good growth was obtained in Vancouver using the culture medium shown in Table 2 (pers. comm. Stein, 1968).

Table 2. Culture medium for zoochlorella from the giant scallop (courtesy Dr. M. Chihara).

Sea water	100.0 ml
$NaNo_3$	0.20 g
$NaH_2PO_4 \cdot 12H_2O$	0.025 g
Trace elements	2.00[1]

([1]EDTA as Na_2EDTA 3.0 g; $FeCl_3$ 0.08 g; $MnCl_2$ 0.12 g; $ZnCl_2$ 0.015 g; $CoCl_2$ 0.003 g; $CuCl_2$ 0.0012 g; NaMO 0.05 g; H_3BO_3 0.60 g).

The St. John's cultures did not survive a power failure and the consequent shut-off of the Psycrotherm. The Vancouver culture is the only surviving one.

RESULTS

Density surveys

The results of the density surveys are shown in Table 3. The survey by underwater observation indicates a relatively higher average density for the Fox Island River bed (4.0 scallops per sq. m) than for the Boswarlos bed (2.3 scallops per sq. m). Scallops appeared to be well distributed on the beds and there was no evidence of clumping by age. There was, however, a marked absence of young scallops 2 yrs and under.

Table 3. Densities of giant scallops on the Boswarlos and Fox Island River beds, Port au Port Bay, Newfoundland.

Location	No. of dives	Total No. of scallops collected	Mean density per sq. m	Frequency of age distribution													
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Boswarlos	31	71	2.26	0	0	2	4	7	10	4	2	17	12	10	2	1	0	0
Fox Is. River	18	112	4.00	0	0	0	2	7	15	9	16	30	15	13	3	2	0	0

Validation of ageing method

Scallops from the shallow waters of Port au Port Bay are comparatively clean and show prominent growth rings especially on the left valve. Interpretation of growth rings on the shell from the bay was further

aided by the relative absence of crustose corallines and strong shock rings, the latter characteristic of heavily fished populations. When present, Lithothamnion growth was often restricted to the umbonal region of the left valve. The time of formation of the annual ring appears to vary from year to year but generally occurs between April and May.

The ageing method has been validated by tagging. Each of 12 scallops recovered after a year had added one ring on the shell. Two additional tagged specimens, recovered after being at large for two years, had each laid down two growth rings.

Age at formation of first annulus

Examination of a large number of scallops under 60 mm indicates that the first visible ring is not laid down in the first year of life but rather during the second. Several small specimens measuring under 20 mm in shell-height were obtained during the summer of 1966 which did not possess a recognizable growth ring (Fig. 4). A scallop caught in July, for example, showing only widely spaced concentric circuli is considered as in its first year of life and its age is designated simply as 0^+. If September 1st is arbitrarily considered as the birthdate of the scallop in Port au Port Bay, then the first visible ring is not laid down until after 18 to 19 months and at the end of the second winter. In this investigation age I^+ designates a scallop about 18 to 19 months old and, therefore, nearly 2 yrs old. The behaviour of spring-spawned scallops (p. 94) remains unknown.

Supernumerary or even faint annual rings may occasionally appear on 0^+ scallops but these are not generally retained and do not show up on older scallops.

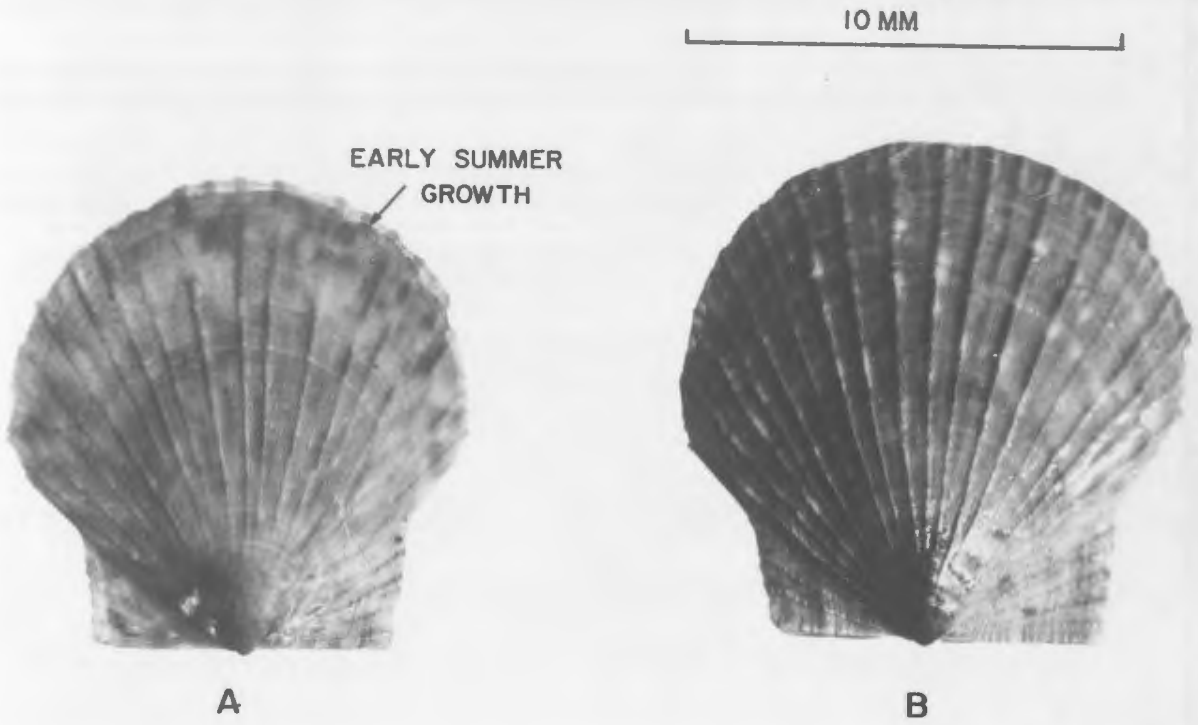


Fig. 4. Juvenile scallops in their first year of growth. Specimen (A) was taken in May and specimen (B) in July. There is no evidence of a discrete annulus in either one of the shells.

Age composition

Age-frequency histograms, expressed as percentages of the totals, are shown in Fig. 5A, B and C for the Boswarlos bed during the years 1966-68. Scallops are equinumerical in sex distribution and are therefore combined in the age-frequency histograms. The same relationship was maintained during the three successive years of observation. The age frequency shows clearly that recruitment of juveniles to the adult stock is quite irregular and varies from year to year. The 1955, 1956, 1960 and 1962 year-classes are particularly well represented on the Boswarlos bed. The scarcity of scallops of the 1958 year-class is striking.

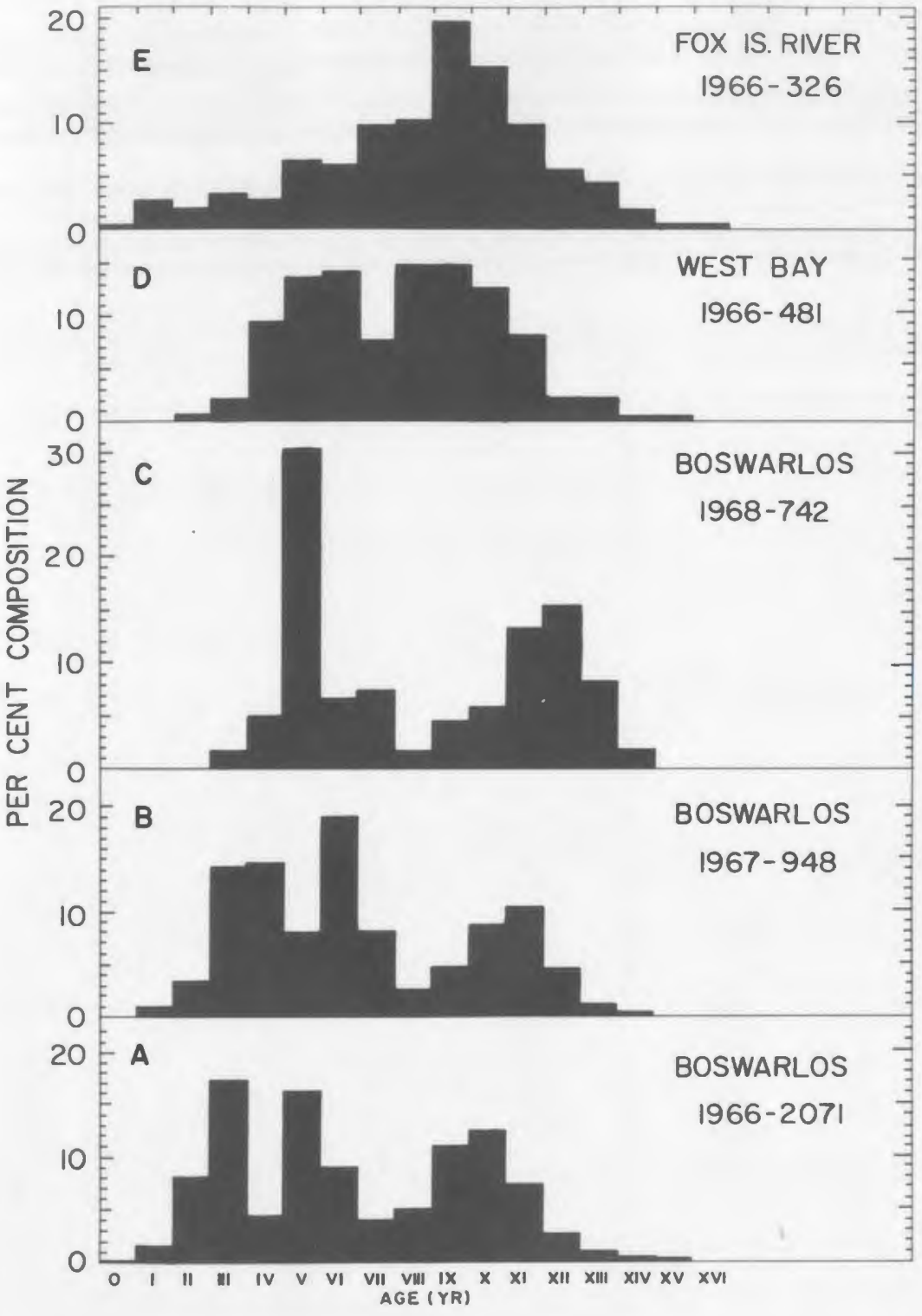


Fig. 5. Age composition of scallops from selected beds in Port au Port Bay, Newfoundland during 1966-68. Number of scallops used in the construction of the histograms is indicated.

Age-frequency histograms for the West Bay and Fox Island River beds are shown in Fig. 5D and E respectively. Again the 1958 year-class is poorly represented on the West Bay bed. The scallops on these beds are generally older than those of the Boswarlos bed and are dominated by the VIII-, IX- and X-year-olds.

The age frequencies on the three principal beds also emphasize the paucity of 0^+ and I^+ scallops. The oldest scallop encountered during the study came from the Fox Island River bed and is estimated to be 16 years old.

Shell-height frequency

The shell-height frequencies of scallops encountered on the three beds in Port au Port Bay in 1966 and 1967 are shown in Fig. 6A-D and summarized in Table 4. The 1966 and 1967 shell-height data for the Boswarlos bed are plotted separately (Fig. 6A and B). The data plotted in 1 mm groups (curve I) exhibit considerable fluctuations. Much of these fluctuations are removed by grouping the data in 5 mm groups and expressing them as percentages of the total (curves II and III). The modes are now widely separated especially in the lower shell-height groups but become progressively more crowded towards the upper range of the distributions. All the height frequencies are those of the distances measured along the curvature of the left valve except for the 1966 Boswarlos collection where the straight tangential heights are superimposed for comparison (Fig. 6A, curve III). Apart from a lag in the tangential heights, both the frequency distributions are similar. The relation between dorso-ventral height (DV)

measured tangent to the shell and the distance from the umbo to the shell margin of left valve measured along the shell curvature (DC) for the three scallop beds are shown in equations 2, 3 and 4.

1. Boswarlos DC = 1.17DV - 5.56 . . . . . (2)
2. West Bay DC = 1.19DV - 7.11 . . . . . (3)
3. Fox Is. River DC = 1.14DV - 3.15 . . . . . (4)

These equations may be used for making conversions from the tangent measurement to that along the curvature, or *vice versa* for samples of scallops collected from any of the three stations.

From the size-frequency distributions of scallops on the Boswarlos bed (Fig. 6A and B), it may be seen that there are relatively few scallops of the 0-40 and 170-185 mm size classes. A general scarcity in the number of scallops occurs between 90-115 mm in 1966 and the same depression appears between 110-122 mm in the following year. However, there are definite modes in the height-frequency distribution curves. In 1966, for example, these modes occur at about 78, 118 and 148 mm (or at 73, 108 and 133 mm when measured tangentially). A smaller mode appears at around 53 mm. The progression of the 3 principal modes into the next year is clear, the first mode having moved to about 103 mm, the second to 128 mm and the final mode has shifted somewhat less from approximately 148 to 153 mm. The small mode occurring about 53 mm in 1966 cannot be easily discerned in 1967; for it has merged with the peak beyond it thereby losing its identity. The height-frequencies of individual age groups for ages I to VIII inclusive are shown in Fig. 7. There is a great

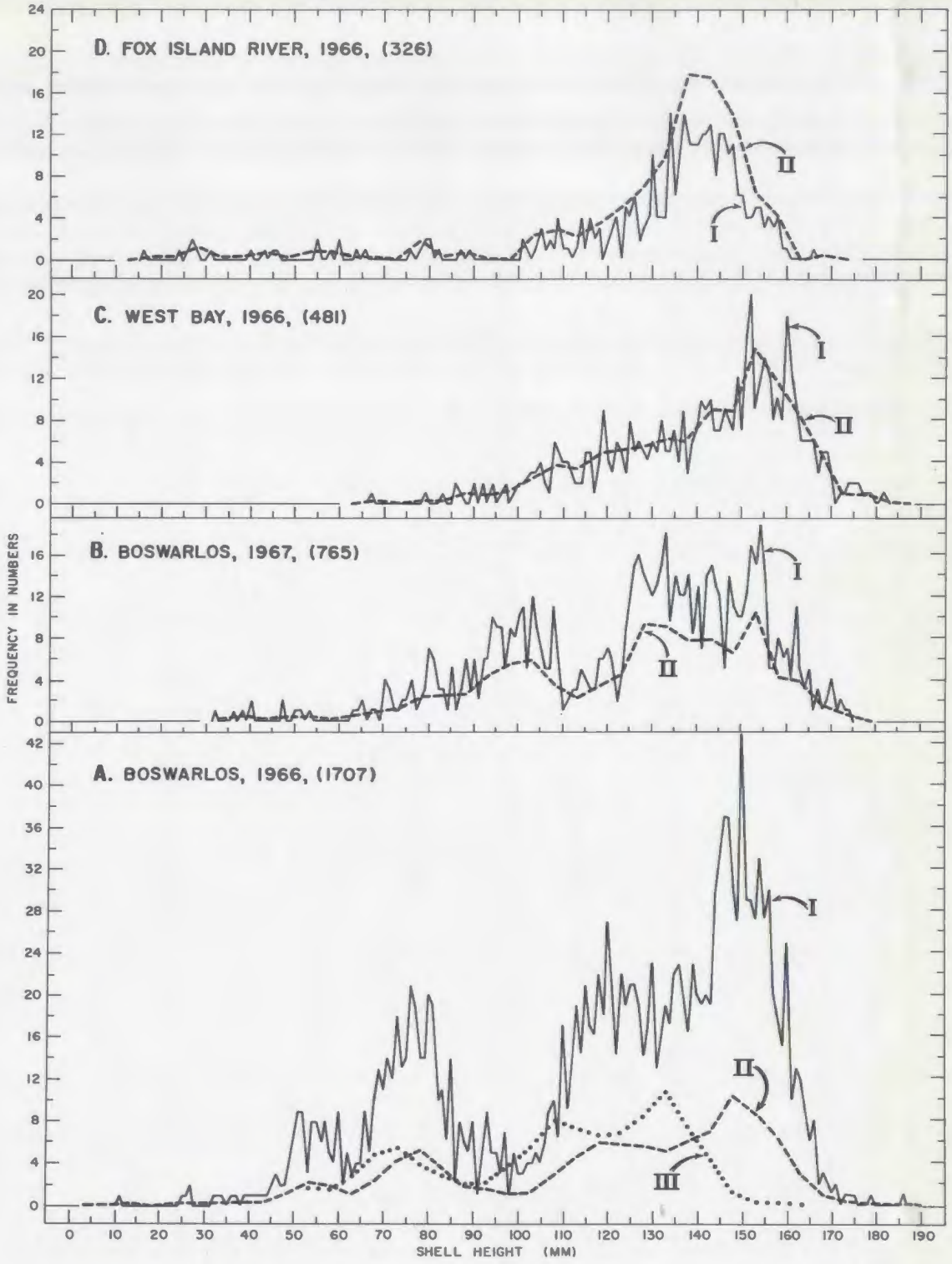


Fig. 6. Shell-height frequencies of scallops from selected beds in Port au Port Bay, Newfoundland during 1966-67. I. Frequency in numbers of curvature shell-height plotted in 1 mm groups; II and III. Percentage frequency of curvature and tangential shell-heights respectively plotted in 5 mm groups and drawn to the same scale as the frequency in numbers. Figures in parenthesis indicate the number of scallops used in the construction of the frequency polygons.

Table 4. Shell-height frequency distribution of scallops grouped in 5 mm intervals in Port au Port Bay, Newfoundland during the years 1966 and 1967. Figures in parenthesis indicate corresponding percentages of the totals.

	FREQUENCY				
	Distance along arc (DA)				Tangential distance (DV)
Shell-	Boswarlos		West Bay	Fox Is. River	Boswarlos
height	1966	1967	1966	1966	1966
1-5	-	-	-	-	
6-10	-	-	-	-	
11-15	1(0.06)	-	-	-	1(0.05)
16-20	-	-	-	1(0.31)	1(0.05)
21-25	1(0.06)	-	-	1(0.31)	3(0.14)
26-30	3(0.18)	-	-	4(1.23)	1(0.05)
31-35	3(0.18)	1(0.13)	-	1(0.31)	6(0.29)
36-40	3(0.18)	4(0.52)	-	1(0.31)	3(0.14)
41-45	5(0.29)	-	-	2(0.61)	15(0.72)
46-50	18(1.05)	3(0.39)	-	1(0.31)	36(1.73)
51-55	37(2.17)	2(0.26)	-	2(0.61)	37(1.79)
56-60	32(1.87)	-	-	3(0.92)	34(1.64)
[illegible]	[illegible]	4(0.52)	-	1(0.31)	61(2.94)

76-80	88(5.16)	17(2.22)	1(0.21)	6(1.84)	80(3.86)
81-85	60(3.51)	18(2.35)	1(0.21)	1(0.31)	57(2.75)
86-90	29(1.70)	19(2.48)	5(1.04)	2(0.61)	39(1.88)
91-95	25(1.46)	33(4.31)	4(0.83)	-	43(2.08)
96-100	19(1.11)	41(5.36)	6(1.25)	-	79(3.81)
101-105	20(1.17)	44(5.75)	12(2.49)	7(2.15)	114(5.50)
106-110	48(2.81)	27(3.53)	18(3.74)	9(2.76)	165(7.97)
111-115	77(4.51)	17(2.22)	16(3.33)	7(2.15)	149(7.19)
116-120	100(5.86)	25(3.27)	23(4.78)	11(3.37)	136(6.57)
121-125	98(5.74)	34(4.44)	25(5.20)	16(4.91)	141(6.81)
126-130	94(5.51)	70(9.15)	26(5.41)	22(6.75)	171(8.26)
131-135	86(5.04)	69(9.02)	30(6.24)	32(9.82)	221(10.67)
136-140	102(5.98)	59(7.71)	29(6.03)	58(17.79)	150(7.24)
141-145	120(7.03)	60(7.84)	43(8.94)	57(17.48)	85(4.10)
146-150	176(10.31)	50(6.54)	43(8.94)	45(13.80)	24(1.16)
151-155	145(8.49)	78(10.20)	71(14.76)	21(6.44)	1(0.05)
156-160	107(6.27)	31(4.05)	56(11.64)	13(3.99)	2(0.10)
161-165	50(2.93)	28(3.66)	40(8.32)	-	1(0.05)
166-170	16(0.94)	11(1.44)	22(4.57)	1(0.31)	-
171-175	5(0.29)	5(0.65)	4(0.83)	-	-
176-180	1(0.06)	-	4(0.83)	-	-
181-185	-	-	1(0.21)	-	-
186-190	1(0.06)	-	-	-	-
TOTALS	1707(100)	765(100)	481(100)	326(100)	2071(100)

amount of overlap of shell-heights with age. The modes are widely separated in the lower age groups but become progressively more crowded in the older scallops.

Although a higher proportion of smaller scallops is found in the Fox Island River bed, there is only one major peak at approximately 138 mm, a subsidiary peak occurring at 108 mm. Scallops below 67 mm in shell-height were not obtained from the West Bay bed. Like the Fox Island River bed there is only one principal mode at 153 mm, subsidiary modes occurring at about 108 and 143 mm. Both the Fox Island River and West Bay beds may be considered to have unimodal height-frequency distributions.

Growth in shell dimensions

Von Bertalanffy growth curves are plotted separately for male and female scallops from the Boswarlos bed (Fig. 8). The curves do not reflect a sex difference in growth. Equations (5) and (6) show the relationships between shell-height measured along the curvature of the left valve and age of male and female scallops. Similar trial plots for the West Bay and Fox Island River beds showed that the differences between

$$\text{Males} \quad l_t = 171.2\,[1-e^{-0.21(t-0.35)}] \quad \ldots\ldots\ldots \quad (5)$$

$$\text{Females} \quad l_t = 171.7\,[1-e^{-0.22(t-0.40)}] \quad \ldots\ldots\ldots \quad (6)$$

the sexes were not sufficient to consider the growth rates separately. In the rest of the section on growth, the sexes have been pooled. Fig. 9A shows the weighted von Bertalanffy growth curves fitted to age at shell-height

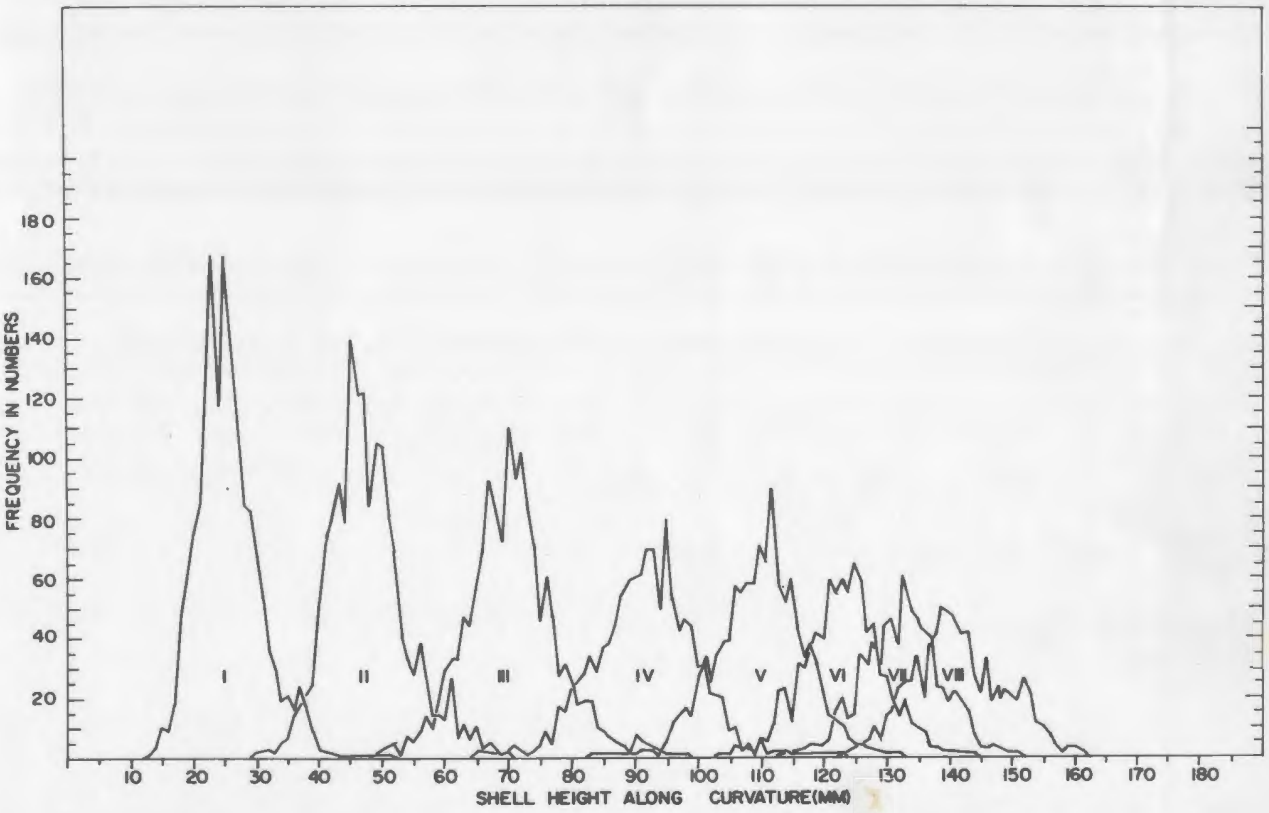


Fig. 7. Shell-height frequency of individual age groups for ages I^+ to $VIII^+$, inclusive.

measured along the curvature of left valves and fitted by the method of Allen (1966a). The range of ages to which the curves were fitted is shown in the summary table (Table 5), but all curves are extrapolated to beyond sample ages up to a maximum of 20 yrs.

The weighted von Bertalanffy growth equations for the three Port au Port scallop beds are as follows:

Boswarlos $l_t = 171.7\ [1-e^{-0.215(t-0.369)}]$ . . . . . (7)

West Bay $l_t = 181.5\ [1-e^{-0.208(t-0.093)}]$ . . . . . (8)

Fox Is. River $l_t = 152.4\ [1-e^{-0.285(t-0.546)}]$ . . . . . (9)

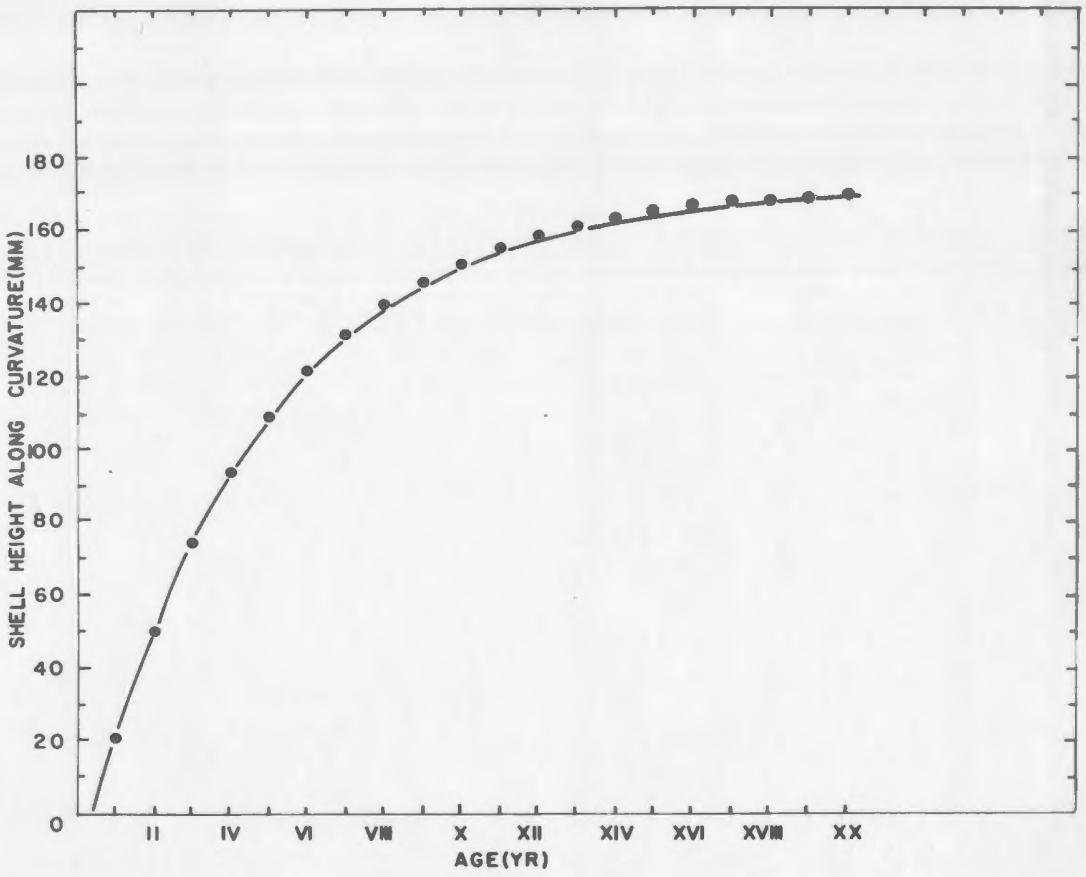


Fig. 8. Von Bertalanffy growth curves for male giant scallop from the Boswarlos bed. The calculated points for females are also indicated.

The von Bertalanffy equations fit the observed shell-height at age data well. The parameters for all the curves fitted by Allen's method together with their 95% confidence limits are summarized in Table 5.

Table 5. Summary table showing weighted von Bertalanffy parameters and their 95% confidence limits for *P. magellanicus* in Port au Port Bay, Newfoundland (Allen's fit).

Location and sex		Parameter			Fitted years
		L_∞	K	to	
Boswarlos	Males	171.2 ± 3.46	0.213 ± 0.013	0.346 ± 0.099	1-15
	Females	171.7 ± 3.41	0.220 ± 0.015	0.401 ± 0.136	1-15
	Sexes combined	171.7 ± 2.39	0.216 ± 0.010	0.369 ± 0.078	1-15
West Bay	Males	181.1 ± 17.47	0.204 ± 0.071	-0.023 ± 0.892	2-13
	Females	180.5 ± 13.90	0.218 ± 0.070	0.257 ± 0.911	3-15
	Sexes combined	181.5 ± 10.91	0.208 ± 0.048	0.093 ± 0.630	2-15
Fox Is. River	Males	149.0 ± 9.78	0.337 ± 0.128	0.920 ± 0.870	3-14
	Females	151.2 ± 9.66	0.339 ± 0.141	0.855 ± 1.034	1-16
	Sexes combined	152.4 ± 5.29	0.285 ± 0.063	0.546 ± 0.670	1-16

The mean shell-height at each annulus along the shell curvature was also computed and the unweighted averages employed to fit the observed shell-height at age data (Fig. 9B). The appropriate von Bertalanffy relationships are indicated in equations 10, 11 and 12.

Boswarlos $l_t = 179.3\ [1-e^{-0.20(t-0.30)}]$ . . . . . (10)

West Bay $l_t = 185.4\ [1-e^{-0.21(t-0.34)}]$ . . . . . (11)

Fox Is. River $l_t = 159.1\ [1-e^{-0.22(t-0.19)}]$ . . . . . (12)

The von Bertalanffy parameters derived from the two methods are compared in Table 6.

Table 6. Comparison of von Bertalanffy parameters derived from the two methods of fit (I) Allen's method (II) Lal's method.

Location	Parameter					
	L_∞		K		to	
	I	II	I	II	I	II
Boswarlos	171.7 ± 2.39	179.3	0.216 ± 0.010	0.195	0.369	0.297
West Bay	181.5 ± 10.91	185.4	0.208 ± 0.048	0.207	0.093	0.338
Fox Is. River	152.4 ± 5.29	159.1	0.285 ± 0.063	0.224	0.546	0.189

Irrespective of the method employed in fitting the equations, the K values are more or less constant but Lal's fit gives consistently higher L_∞ values.

The growth curve for the Boswarlos sample is also plotted using the conventional tangential mean distances to each annulus and is shown in Fig. 10 together with curves computed for other areas from published data. The growth parameters of the giant scallop from the several selected

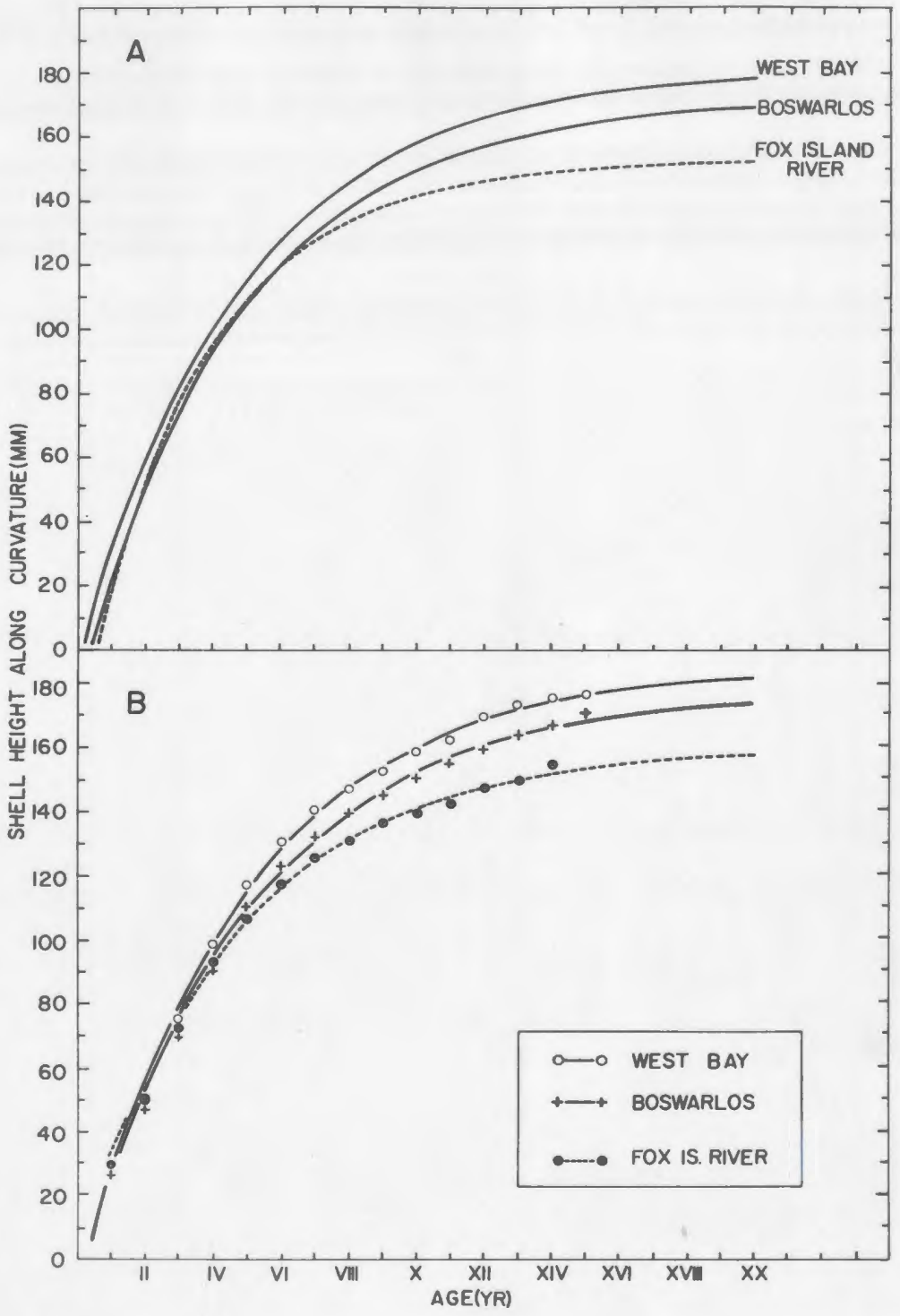


Fig. 9. A. Weighted von Bertalanffy growth curves fitted to curvature shell-height at age (Allen's method).

B. Unweighted von Bertalanffy growth curves fitted to mean curvature shell-height at age (Lal's method).

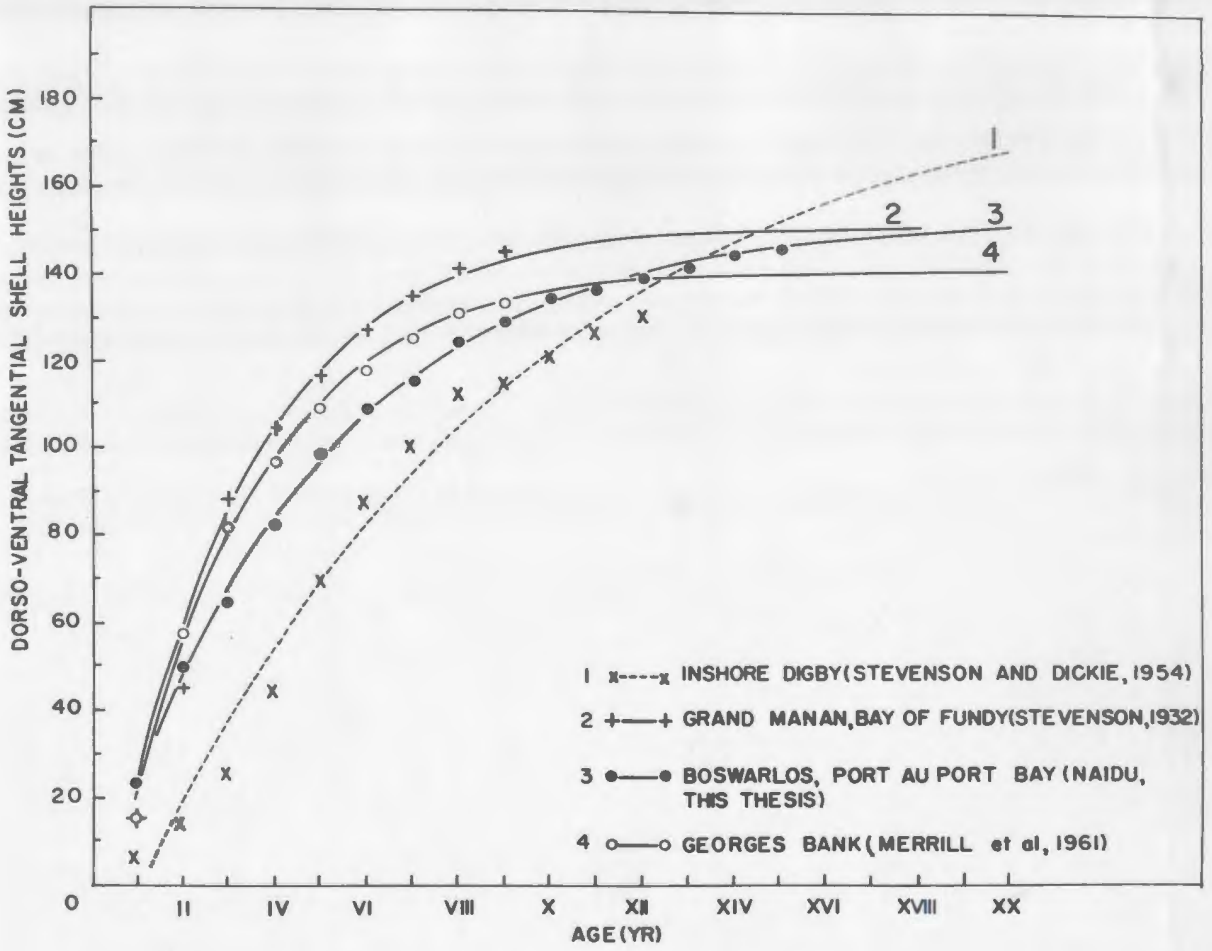


Fig. 10. Comparison of von Bertalanffy growth curves of scallops from different areas computed by using conventional tangential dorso-ventral mean shell-heights to annuli.

areas are summarized for comparison (Table 7). There are considerable differences in the growth pattern of scallops from the different areas examined. The data of Stevenson and Dickie (1954) do not appear to fit a von Bertalanffy type of growth curve. If the unrealistic L_∞ value computed for Stevenson's and Dickie's data is ignored, then a general trend in L_∞ values

with latitude may be seen. Scallops from the more northerly latitudes appear to reach larger sizes than those from the south. K values, on the other hand, decrease with increasing latitude.

Table 7. Von Bertalanffy growth parameters of the giant scallop from selected areas in the northwest Atlantic. The sources of the data used in the computations are shown in parenthesis.

Area	Latitude North	Parameter L_∞	K	to	Fitted years
Georges Bank (Merrill *et al.*, 1961, Reader No. 1, p. 310)	41° 52'	141.4	0.343	0.559	1-9
Grand Manan, Bay of Fundy (Stevenson, MS, 1932, p. 17)	44° 42'	151.1	0.356	0.676	1-9
Digby, Bay of Fundy, N.S. (Stevenson, MS, 1932, p. 17)	44° 42'	149.3	0.281	0.436	1-9
Digby, Bay of Fundy, N.S. (Stevenson and Dickie, 1954, p. 668)	44° 42'	190.1	0.117	1.133	1-12
Boswarlos, Port au Port Bay, Nfld. (this thesis)	48° 40'	153.2	0.211	0.236	1-15

Fig. 11A, B and C show the von Bertalanffy growth curves for the total dorso-ventral axis (tangential measure), the anterior-posterior axis and the wing base respectively. These curves were fitted to unweighted mean size at age, and the parameters are summarized in Table 8. Again the

Table 8. Summary of von Bertalanffy parameters for the (A) tangential dorso-ventral axis, (B) anterior-posterior axis and (C) wing base of the left valve of scallops from three selected beds in Port au Port Bay (Lal's fit).

Shell character	Parameter			Fitted years
	L_∞	K	to	
(A) Dorso-ventral axis				
1. Boswarlos	152.38	0.206	-0.477	1-15
2. West Bay	160.50	0.189	-0.878	1-14
3. Fox Is. River	139.93	0.265	0.106	1-15
(B) Anterior-posterior axis				
1. Boswarlos	169.06	0.177	-0.635	1-15
2. West Bay	174.86	0.190	-0.501	1-14
3. Fox Is. River	149.52	0.253	0.220	1-15
(C) Wing base				
1. Boswarlos	94.63	0.171	-0.487	1-15
2. West Bay	97.20	0.210	0.192	1-14
3. Fox Is. River	70.44	0.307	0.223	1-15

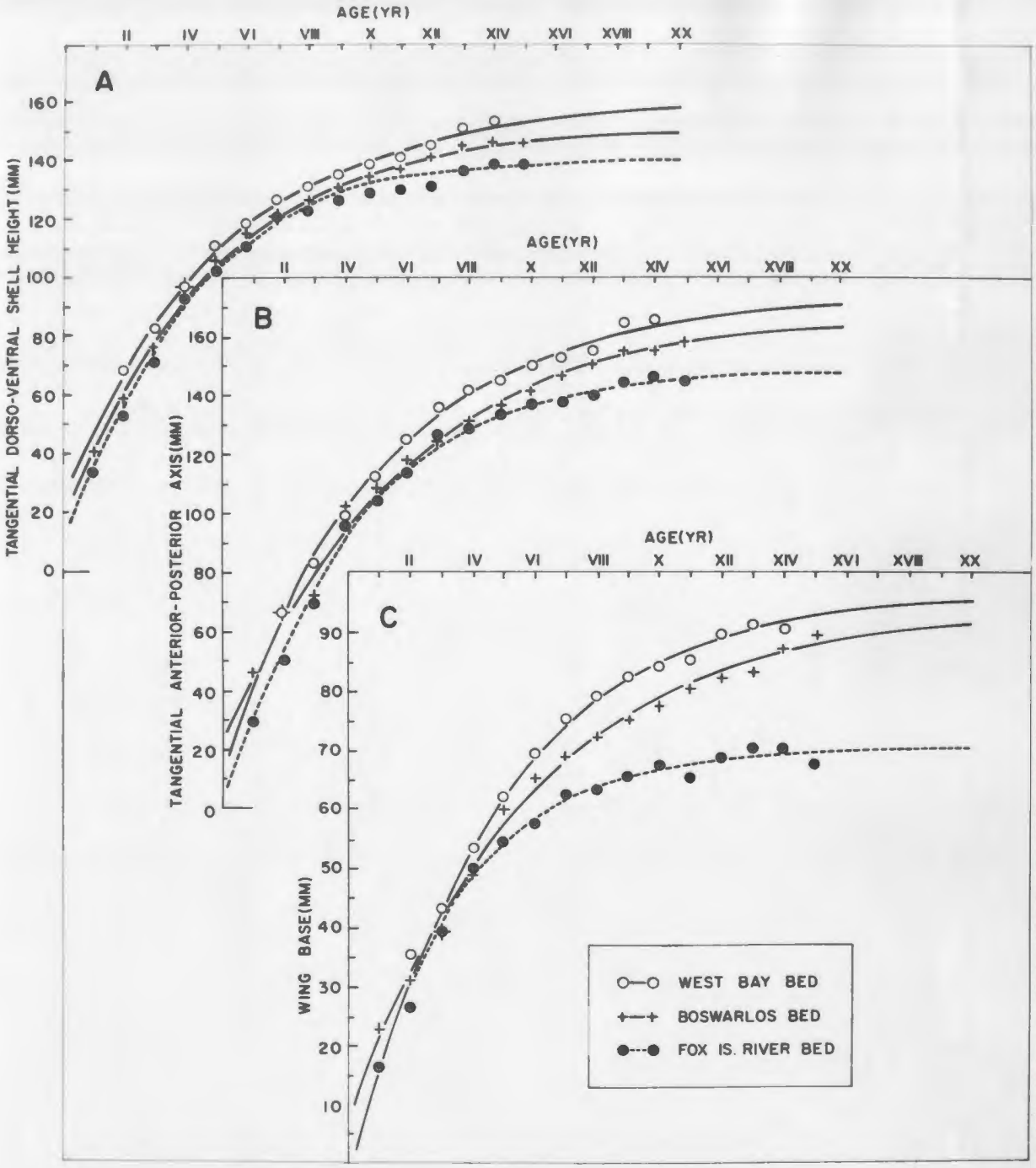


Fig. 11. Unweighted von Bertalanffy growth curves fitted to selected shell dimensions of the giant scallop from three major scallop beds in Port au Port Bay, Newfoundland.

curves are extrapolated beyond sample ages up to 20 yrs. It is emphasized here that these curves do not employ the mean size at each annulus but rather the total average shell dimension at age and, therefore, include various amounts of shell growth beyond the last formed annulus.

Scallops from the West Bay bed attain greater dimensions in all three shell characters selected for study, while those from the Fox Island River bed are smaller in respect to each of these shell characters. Regardless of the potential maximum average size attainable by the population (L_∞) with respect to any one of these shell characters, the K values for any one of these shell characters within any one bed remain fairly constant.

Increase in shell weight

Mean dry shell weights at age of scallops from the three areas are shown in Table 9. It is clear that, not only do Fox Island River scallops grow more slowly, but also that they possess characteristically light shells. The dry shell-adductor muscle weight ratio is relatively high on this bed, often reaching values of 0.2 to 0.3.

Table 9. Average dry shell weight at age of scallops from Port au Port Bay, Newfoundland. Figures in parenthesis indicate number of scallops used in computing the means.

Age (yr)	Mean shell weight in gm		
	West Bay	Boswarlos	Fox Is. River
I+	-	11.0(9)	-
II+	29.0(1)	23.8(36)	-
III+	39.0(1)	43.9(44)	33.0(5)
IV+	78.9(31)	72.6(11)	70.7(9)
V+	108.8(43)	116.7(47)	95.5(13)
VI+	146.0(38)	139.2(16)	104.5(8)
VII+	182.8(17)	137.5(4)	130.0(15)
VIII+	199.0(28)	186.4(16)	138.1(13)
IX+	227.0(24)	192.9(28)	139.1(26)
X+	259.3(10)	210.2(35)	128.1(13)
XI+	247.6(9)	215.4(19)	-
XII+	237.5(2)	220.5(8)	116.7(3)

Adductor muscle weight relationships

The relationship between the posterior adductor muscle weight and age of the scallop is not linear, but it was evident that an approximately linear relationship could be obtained by using the regression of adductor muscle weight on the logarithm of age, and in the comparisons below semi-logarithmic regressions of this type have been used. All between area

comparisons are based on scallops without reference to an algal infection of the molluscan tissues which adversely affect the soft parts of the animal; this is, however, discussed elsewhere in this paper.

Seasonal variations in adductor muscle weight

In order to compare the relationship of adductor muscle weight with age of scallops from different areas it was first necessary to ascertain if there were any seasonal changes in the adductor muscle weight within any one area. The monthly variation in adductor muscle weight as a function of age was investigated for uninfected scallops from the Boswarlos bed for the months May to November 1966. Figure 12 shows the regressions of adductor muscle weight on log age for each of the months examined. The regression equations are summarized in Table 10. To test if the individual regression

Table 10. Regression equations of adductor muscle weight (Wm) on log age (t) for uninfected Boswarlos scallops collected monthly from May to November 1966.

May	$Wm = 48.4 \log t - 12.21$	(13)
June	$Wm = 51.2 \log t - 16.28$	(14)
July	$Wm = 43.5 \log t - 11.76$	(15)
August	$Wm = 45.3 \log t - 12.90$	(16)
September	$Wm = 40.4 \log t - 8.30$	(17)
October	$Wm = 49.2 \log t - 13.34$	(18)
November	$Wm = 48.7 \log t - 12.99$	(19)

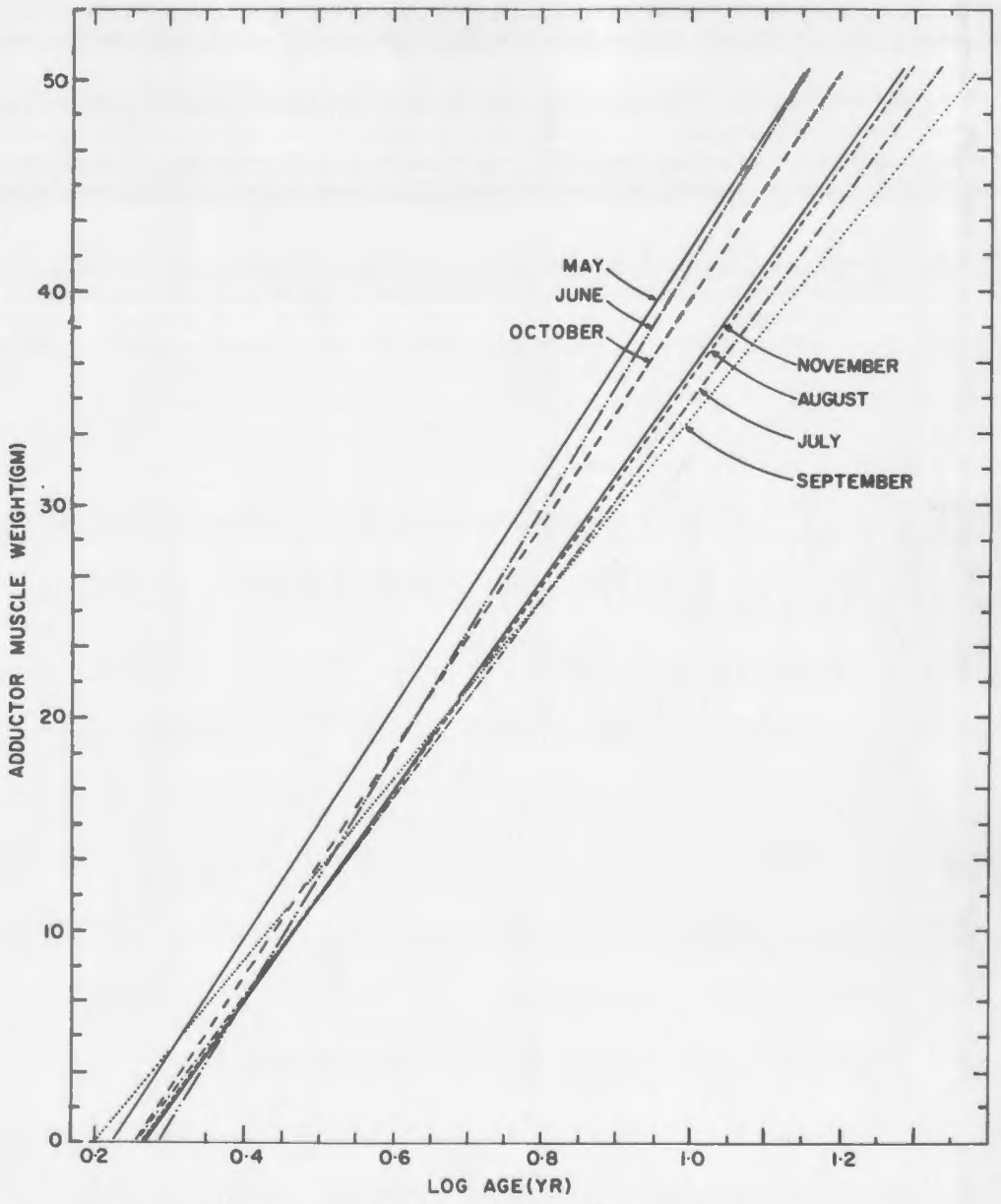


Fig. 12. Weighted monthly adductor muscle weight-log age regression lines of the giant scallop from the Boswarlos bed, Port au Port Bay, Newfoundland for the period May-November 1966 (Equations 13-19).

lines differ significantly the data were examined by an analysis of covariance. A highly significant difference between the slopes was indicated (Table 11).

Table 11. Analysis of covariance of monthly regressions of adductor muscle weight on log age.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	2412	58360.27	24.20
REG. COEFF.	6	1801.13	300.18
COMMON	2418	60161.40	24.88
ADJ. MEANS	6	2863.90	477.32

Comparison of slopes F = 12.41

Probability of random occurrence 0.001**

Relationship between adductor muscle weight and age of Boswarlos, West Bay, and Fox Island River scallops

As there were monthly differences in the adductor muscle weights only August collections were used in the between bed comparisons. This was the only month for which samples were available for all areas to be compared. As we are investigating possible locality differences in the adductor muscle weight it was again thought desirable to include both infected and uninfected scallops in these comparisons. Figure 13 shows the regressions of adductor muscle weight on log age for the three principal scallop beds in Port au Port Bay. The following weighted least squares equations have been calculated:

Boswarlos $Wm = 41.9 \log t - 10.36$ . . . . . (20)

West Bay $Wm = 54.7 \log t - 16.10$ . . . . . (21)

Fox Is. River $Wm = 55.7 \log t - 19.98$ . . . . . (22)

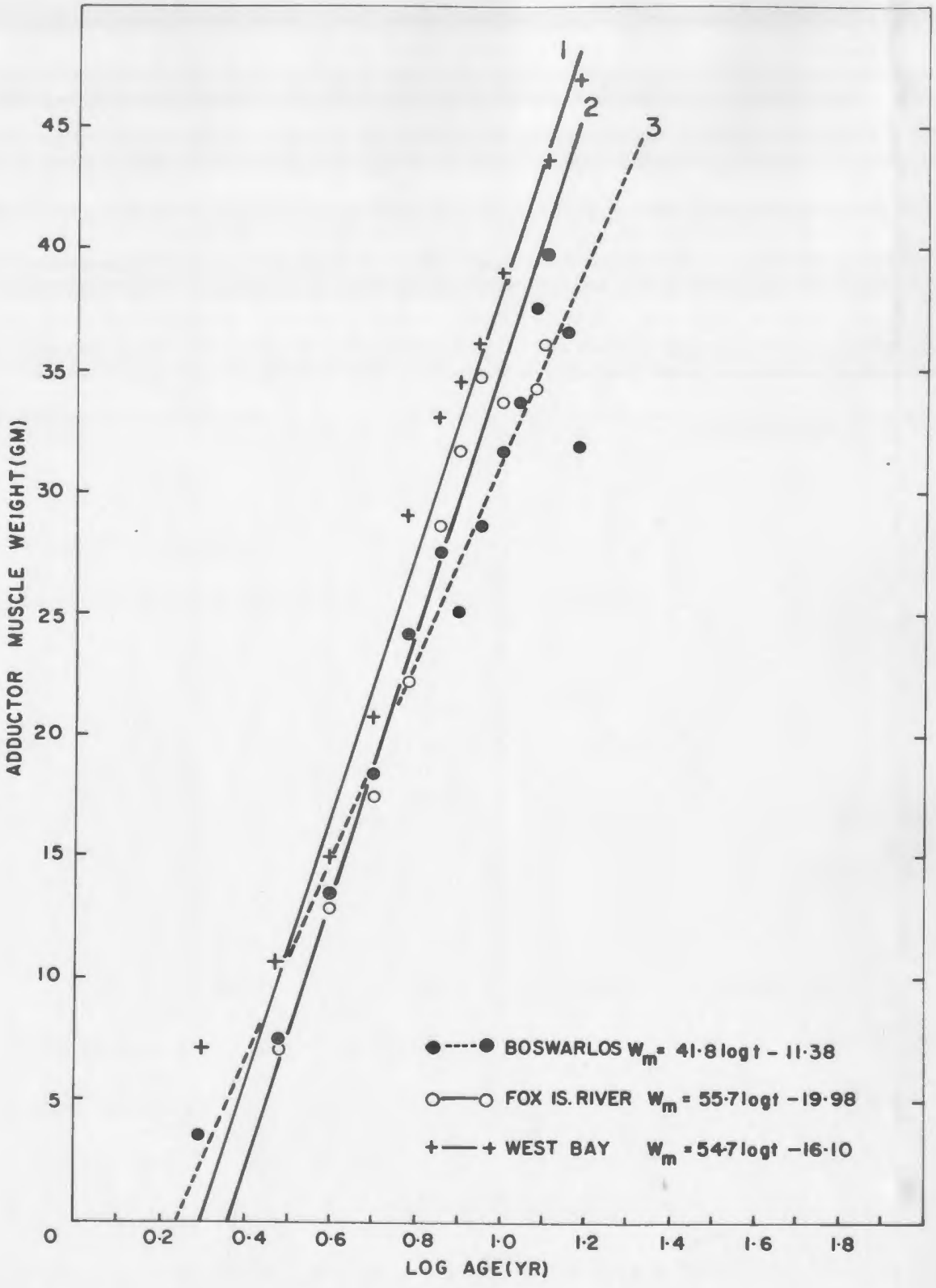


Fig. 13. Weighted adductor muscle weight-log age regression lines of the giant scallop from three selected beds in Port au Port Bay, Newfoundland. Mean muscle weights at each age for the three areas are indicated.

An analysis of covariance to test the significance of the difference between the regression lines showed that the difference between the slopes in the regressions of adductor muscle weight on log age is highly significant (Table 12). At comparable ages beyond about six years West Bay scallops have the highest meat yield and those from the Boswarlos bed the lowest. Below this age scallops from the Fox Island River have the lowest meat yield.

Table 12. Analysis of covariance of regression of adductor muscle weight on log age of scallops from Port au Port Bay.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	931	32595.03	35.01
REG. COEFF.	2	1068.42	534.21
COMMON	933	33663.44	36.08
ADJ. MEANS	2	4473.58	2236.79

Comparison of slopes F = 15.26

Probability of random occurrence 0.000**

Table 13 shows the average adductor muscle weight at age and the number of scallops required at each age to yield a pound of commercial meat. Within the age groups the greatest increase in muscle weights occurs between the fifth and sixth years in the Boswarlos and West Bay scallops, when the scallop is between 118-129 mm and 121-134 mm in curvature

Table 13. Meat count per pound of Port au Port Bay scallops. Figures in parenthesis indicate mean adductor muscle weight (gm) at each age.

Age (yr)	Scallop bed		
	Boswarlos	West Bay	Fox Is. River
I+	363(1.25)	-	-
II+	128(3.55)	63(7.20)	-
III+	61(7.40)	43(10.60)	65(7.02)
IV+	34(13.21)	31(14.85)	35(12.82)
V+	25(18.31)	22(20.73)	26(17.41)
VI+	19(24.08)	16(28.95)	20(22.21)
VII+	17(27.46)	14(33.29)	16(28.57)
VIII+	18(25.05)	13(34.41)	14(31.68)
IX+	16(28.59)	13(36.17)	13(34.66)
X+	14(31.55)	12(39.01)	13(33.63)
XI+	13(33.99)	13(33.92)	-
XII+	12(37.48)	11(39.95)	13(34.10)
XIII+	11(39.82)	10(43.80)	-
XIV+	12(33.63)	-	12(36.60)
XV+	14(31.80)	10(47.00)	-

shell-height respectively. The greatest increment in the muscle weight of Fox Island River scallops occurs between the six and seven-year-olds when the scallop is between 122 and 134 mm in shell-height. Beyond the sixth

year scallops from the Boswarlos bed have the lowest meat yield. This roughly corresponds to the point of intersection of the least squares regressions of adductor muscle weight on log age (Fig. 13). Of the three areas examined, the West Bay scallops provide the highest meat yield throughout all age groups.

Adductor muscle scar area relationships

The relationship between the right and left adductor muscle scar areas (SA) with log age (t) is shown in Fig. 14. The least squares regression lines describing the relationship are as follows:

$$\text{Right SA} = 1.76 \log t - 0.29 \quad . \ . \ . \ . \ . \quad (23)$$

$$\text{Left SA} = 2.33 \log t - 0.37 \quad . \ . \ . \ . \ . \quad (24)$$

It may be seen that the scar areas on the two valves are dissimilar and that the difference between them increases with the age of the scallop. Statistically the difference in the regression slopes of the right and left adductor scar areas on log age is highly significant (Table 14). Therefore in the examination of adductor scar areas on age for the three beds only the larger, left adductor scar areas were used. Seasonal changes in left adductor scar areas were not investigated. It is suspected, however, that temporary changes that were observed in the adductor muscle weights are not accompanied by changes in the adductor scar area.

Fig. 15 shows the computed least squares regression lines of left adductor scar area on log age. To test the significance of the difference between the regression lines analysis of covariance was again used. The very

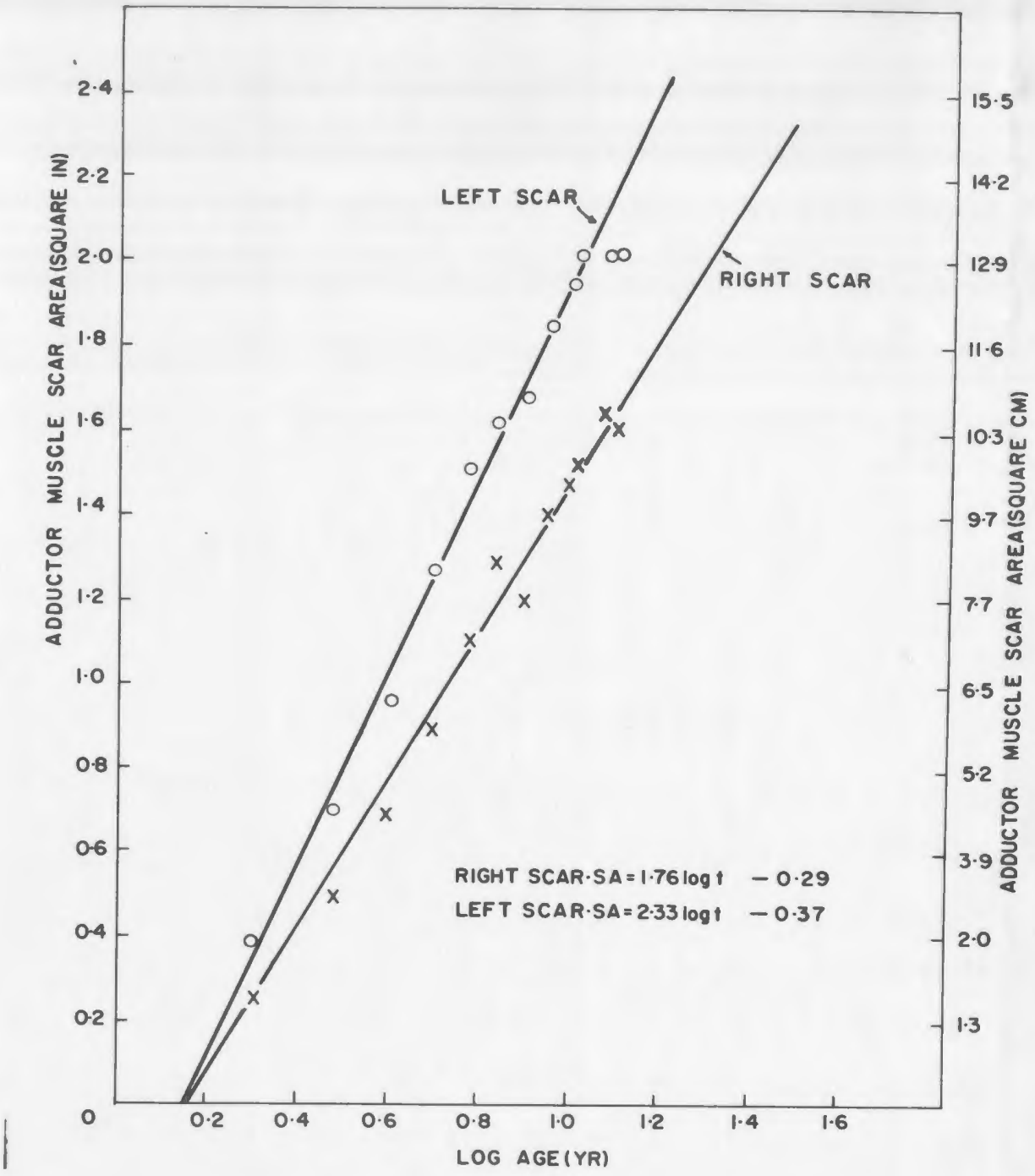


Fig. 14. Weighted adductor muscle scar area-log age regression lines of right and left valves of the giant scallop. The mean scar areas at each age are shown.

significant F values (Table 15) led to a rejection of the hypothesis of a common slope. Thus the muscle scar area relationships of scallops from

Table 14. Analysis of covariance of regression of right and left adductor muscle scar areas on log age.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	789	42.16	0.053
REG. COEFF.	1	2.38	2.38
COMMON	790	44.54	0.056
ADJ. MEANS	1	22.46	22.46

Comparison of slopes F = 44.48

Probability of random occurrence 0.000**

the three beds investigated would be better described by separate regression lines (equations 25, 26 and 27).

Boswarlos SA = 2.28 log t - 0.34 . . . . . (25)

West Bay SA = 2.75 log t - 0.29 . . . . . (26)

Fox Is. River SA = 2.86 log t - 0.58 . . . . . (27)

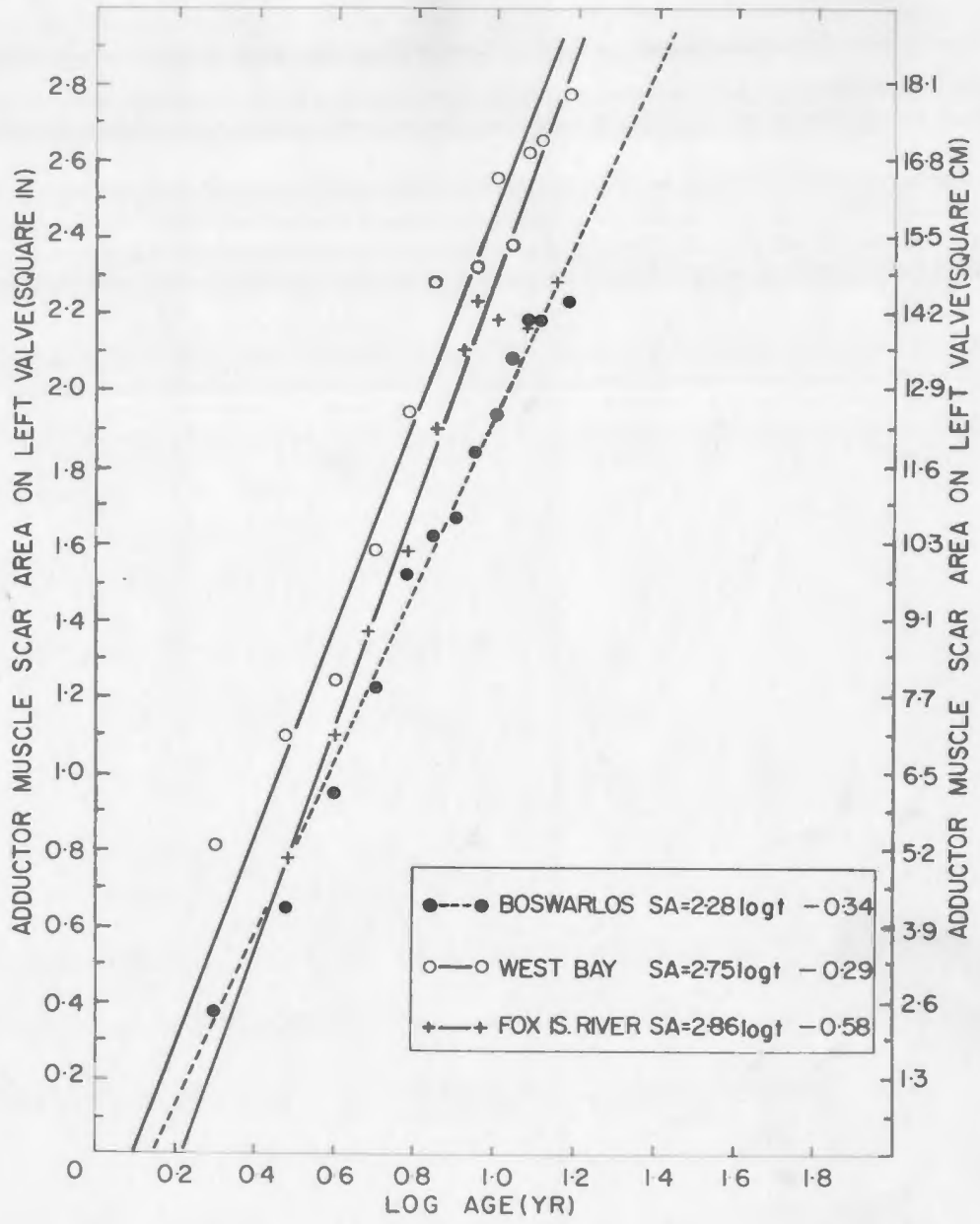


Fig. 15. Weighted left scar areas-log age regression lines of scallops from Port au Port Bay, Newfoundland. Mean scar areas at each age are shown.

Table 15. Analysis of covariance of regression of left adductor muscle scar areas on log age of Port au Port Bay scallops.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	1224	76.98	0.063
REG. COEFF.	2	1.35	0.673
COMMON	1226	78.33	0.064
ADJ. MEANS	2	25.11	12.56

Comparison of slopes F = 10.71

Probability of random occurrence 0.001**

Natural mortality

Of the 96 cluckers used in estimating the average time required for separation, 48 shells (50%) were separated by Oct. 2nd, giving an average period of 70 days. Various types and degrees of separation were observed. Separation was considered complete if gravitational force alone caused the right valve to break off from the hinge line when held by the left valve. There is a gradual loss and finally a complete disappearance of gaping in the valves characteristic of fresh cluckers. At the end of 93 days all cluckers except one had separated.

The annual natural mortality rate was calculated using the formula proposed by Dickie (1955):

$$a = 1-e^{-(C/T)(1/L)(365)}$$

where a is the annual mortality rate

C is the number of cluckers per haul

T is the average time in days required for the valves to separate

L is the number of live scallops per haul

and e is the natural base of logarithms.

The essential computations are shown in Table 16.

The annual natural mortality calculated in this way yielded a rather high value of 18.36%.

Reproductive biology

Structure of the gonad

The gonad of the giant scallop was briefly described by Drew (1906).

The giant scallop is dioecious, having male and female reproductive organs in different animals. The gonad is situated posterior and ventral to the foot and is attached to the posterior adductor muscle at its proximal end. It varies greatly in size and colour throughout the breeding season. The sexes may be easily distinguished by the colour of the sexual products within the tongue-like gonads. The ripe testis is cream in colour and the ovary, when filled, is almost brick-red. The gonad colour is most intense just before spawning suggesting a relationship with the degree of maturity. The gonads undergo a striking increase in thickness as ripeness is approached. When ripe, the gonad is the most conspicuous organ in the scallop and occupies the greater portion of the visceral mass. A loop of the alimentary canal passes through the gonad and may be seen clearly in immature gonads or even in spent adults. Occasionally when the loop passes close to the gonad epithelium it causes a slight protuberance above the general surface.

Table 16. Calculation of natural mortality for the Boswarlos bed, Port au Port Bay, Newfoundland.

Year	No. of hauls	No. of cluckers	No. of living scallops	C	L	T	$\frac{C}{t} \times \frac{1}{L} = i$	it (t = 365 days)	$e^{-it} = S$	Annual natural mortality rate $a = 1-S$
1966	21	73	1900	3.475	90.476	70	0.000549	0.2003	0.8164	0.1836

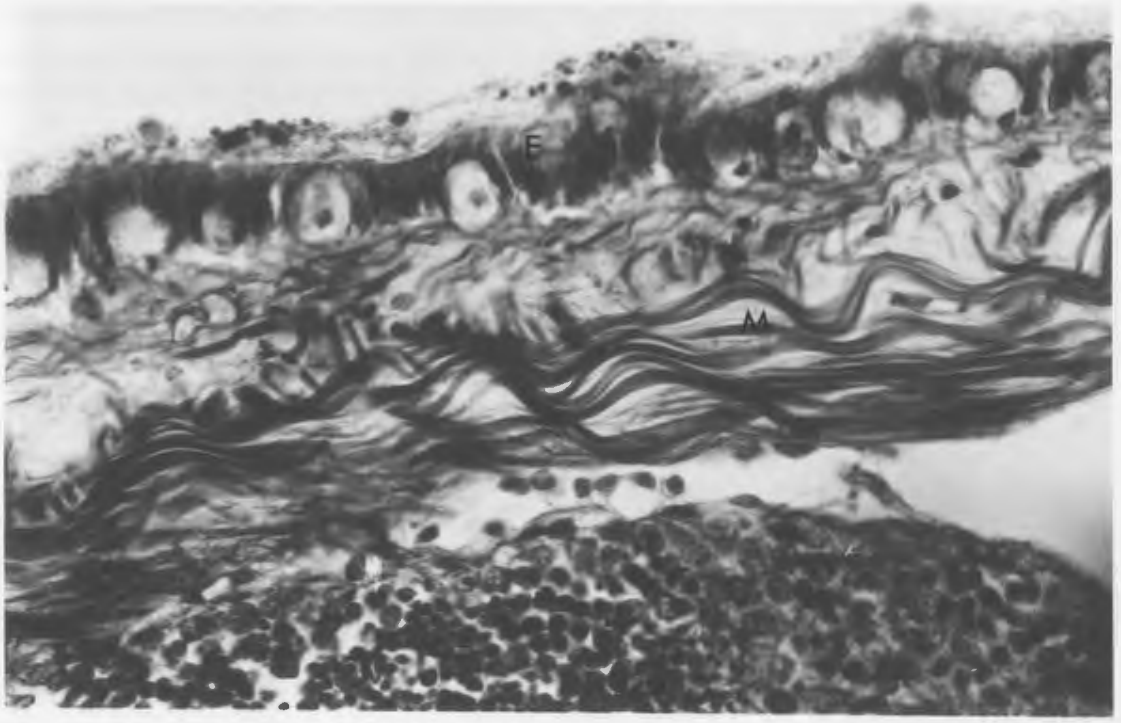


Fig. 16. Outer gonad wall of *P. magellanicus* showing epithelial layer (E) and muscle fibres (M).

In section the gonad may be seen to consist of numerous follicles or alveoli interspersed among branched ciliated tubules or gonoducts. The ducts are usually circular in cross section and vary from several microns to about 1 mm in diameter. Ripe gametes may be seen within the gonoducts in spawning individuals (Fig. 29C). The ramified branches of the gonoducts eventually join up and open into the kidney from where they are discharged into the surrounding water.

The amount of connective tissue present depends on the state of maturity of the gonad. Very little connective tissue is present in the mature, ripe gonad.

The wall of the gonad is made up of an outer epithelium 7-12μ thick and an inner muscular layer ranging in thickness from about 80-130μ (Fig. 16).

A series of transverse muscle fibres 7-80μ in diameter was seen throughout the length of the gonad. Many of these fibres are associated with the muscle fibres of the wall. Contractions of the gonad musculature probably assist in the extrusion of gametes.

In scallops (Pectinidae) as in some other Prionodesmacea, the gonads are composed entirely of gametogenetic cells which receive their nourishment directly from the surrounding vesicular connective tissue (Coe, 1943). The gonad follicles develop at the expense of the nutritive connective tissue or mesenchyme surrounding them.

Sex ratios

The sex ratios of scallops from the three major scallop beds in Port au Port Bay are shown in Table 17.

Table 17. Sex ratios of *P. magellanicus* from selected beds in Port au Port Bay, Newfoundland. The Boswarlos sample represents the combined totals for 1966 and 1967. Figures in parenthesis indicate corresponding percentages.

Bed	Sex frequency			Totals
	Males	Females	Hermaphrodites	
Boswarlos	1509 (50.3)	1453 (48.4)	38 (1.3)	3000
West Bay	87 (40.5)	124 (57.7)	4 (1.9)	215
Fox Is. River	49 (50.0)	49 (50.0)	0 (0.0)	98
Totals	1645 (49.7)	1626 (49.1)	42 (1.3)	3313

A Chi-square test showed that there was no significant difference between the sexes in the overall totals for the bay indicating an equinumerical sex distribution ($X^2 = 0.110$; $P > 0.05$). The ratio of males to females with different size classes of all age groups was also examined (Table 18). The smaller sized groups are predominantly males whereas the larger scallops appear to be dominated by females.

Hermaphroditism

A total of 42 hermaphrodites was encountered during the present investigation giving an overall percentage of 1.3 for the Port au Port area. In almost all cases hermaphrodites were recognized by patches of whitish to cream male follicle cells embedded in a brick-red, predominantly ovarian matrix. The male tissues in hermaphrodites were small, irregular in outline and distributed at random throughout the gonad. Only two gonads with almost equal distribution of sex cells within each gonad were found. In both these scallops the ovary occupied the greater volume of the proximal end of the gonad.

Gametogenesis

Sexual maturation in lamellibranchs can be divided into two classes, one dealing with the development of the primary gonad, and the other with cyclical development of gametes in the adults. This study is chiefly concerned with the latter phase. As in several other molluscs, the sexual products arise by proliferation of the germinal cells which line the follicle walls. As the gonads become mature the follicles become filled with sexual products, normally of one sex. Successive gametogenetic stages

Table 18. Proportion of sexes by shell-height (tangential dorso-ventral axis) grouped in 10 mm intervals.

Location	Year	Sex	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140	141-150	151-160	161-170	Totals
Boswarlos	1966	Male	-	1	4	8	40	54	100	118	52	65	148	136	146	163	39	2	0	1076
		Female	-	0	0	1	10	16	58	72	41	51	127	141	164	201	66	1	0	949
		Hermaphrodites	-	0	0	0	0	0	3	3	2	5	3	6	1	3	4	0	1	31
		Sexes combined	-	1	4	9	50	70	161	193	95	121	278	283	311	367	109	3	1	2056
	1967	Male	0	0	0	3	1	4	18	32	46	46	38	76	66	75	27	1	0	433
		Female	0	0	0	0	3	0	13	19	47	65	36	100	103	81	32	5	0	504
		Hermaphrodites	0	0	0	0	0	0	0	0	1	0	0	1	3	2	0	0	0	7
		Sexes combined	0	0	0	3	4	4	31	51	94	111	74	177	172	158	59	6	0	944

follow the basic pattern characteristic of pelecypod molluscs. Only the more salient features are therefore presented.

Oogenesis. Oogenesis in the giant scallop begins with the appearance of enlarged cells in the germinal epithelium. The oogonia often have large nuclei, with conspicuous nucleoli and loose chromatin network. These cells give rise to oocytes by division. Oocytes often contain fibrillar mitochondrial bodies and spiremes of densely packed chromosomes and possess very conspicuous acentrally placed nucleoli. The oocytes grow rapidly, become enlarged and rounded and protrude into the centre of the follicles. The germinal vesicles may lose some of their chromatin network but retain prominent nucleoli. The mature oocyte in a 10-year-old scallop has a diameter ranging from 80 to 90μ and in sections appear polygonal or hexagonal. Mature ova may be seen undergoing maturation, as shown by the disappearance of the germinal disc. The ova are so closely packed that it is often difficult to distinguish between adjacent follicles.

Spermatogenesis. Sperm formation begins with the presence of a large number of spermatogonia 5-10μ in diameter, lining the wall of male follicles. The sperm are proliferated from spermatogonia on the follicle wall by a series of successive stages (primary and secondary spermatocytes 3-6μ, spermatids 1.5 to 2.0μ and flagellated spermatozoa about 40-50μ occurring in that order centripetally). Each sperm has a conical head measuring about 1.5μ. The proliferating cells are forced into the centre of the follicles while the earlier stages remain close to the follicle wall. Spermatozoa are arranged radially from the centre of the follicle. Early

spermatogenic stages are present, lining the follicle wall throughout development, peripheral spermatogonia becoming prominent immediately after spawning.

Spermatogenesis occurs more rapidly than oogenesis and many spermatozoa are present in the lumen of follicles before the oocytes are fully grown.

Seasonal gonadal changes in the giant scallop

The gonads of the scallop undergo pronounced seasonal changes. The gonad condition during the breeding cycle may be conveniently divided into ten arbitrary stages of maturity (Table 19). This classification is based on the gross macroscopic appearance of the gonad together with the corresponding histological details within them. The method of assigning the state of maturity of the scallop by macroscopic examination of the gonads has the advantage of rapid examination of large numbers of gonads and the division into stages facilitates the presentation of data. While there is some uncertainty in recovering, filling and half-full stages, there is no ambiguity in the full and spent stages, the recognition of which is essential in determining the breeding season. Histological examination of the gonads, on the other hand, is an unfailing method of determining the sexual state of the organism. The criteria used in defining the composite categories are as follows:

Table 19. Macroscopic features and histological details of gonad stages in *P. magellanicus*.

0 Undifferentiated (Immature). Gonad barely visible and inconspicuously small, transparent and colourless;

		discernible only by the intestinal loop within.
		Undeveloped and no differentiation; only loose vascular connective tissue adjacent to the intestinal loop (Fig. 17A).
I	Differentiated (Immature).	Gonad still small and inconspicuous; flat and angular; transparent and colourless; intestinal loop distinct, follicles not visible.
		Most (about 2/3) of gonad occupied by loop of alimentary canal; connective tissue well developed. Beginnings of differentiation and ramification of follicles and ciliated ducts; some primary germ cells on follicle walls (Fig. 17B and C).
		A longitudinal section of the whole gonad at this stage is shown in Fig. 18A.
II	Developing (Virgin).	Gonad slightly larger, translucent but retains flat angular configuration. Loop of alimentary canal visible through outer wall of gonad. Reproductive elements just visible to naked

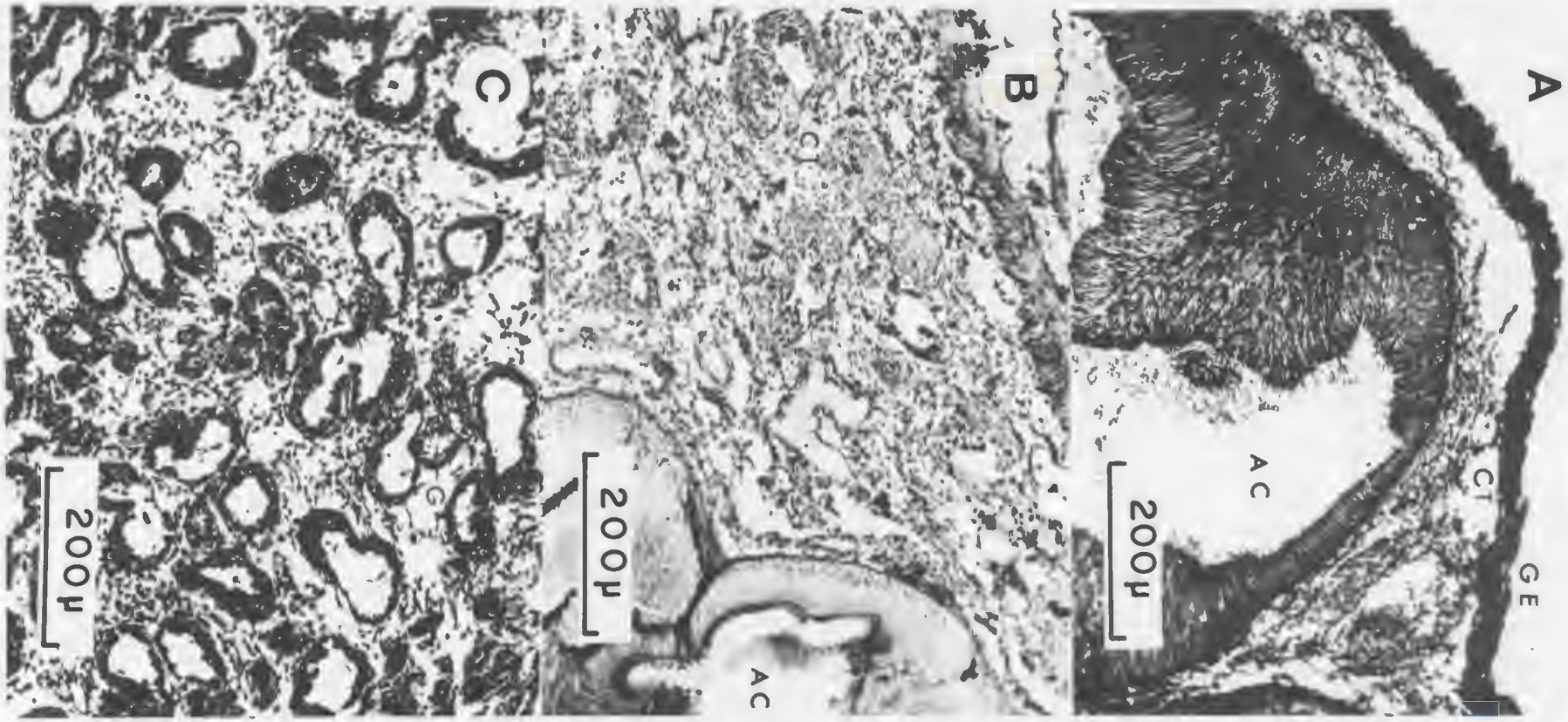


Fig. 17. Description of gonad stages in *P. magellanicus*.

A. Undifferentiated (Immature)

B. Differentiated male (Immature)

C. Differentiated female (Immature)

(GE. Gonad epithelium; CT. Connective tissue; AC. Alimentary canal; G. Gonoduct).

eye; no visible differentiation into testis and ovary.

Much connective tissue between follicles. Synapsis at proximal portion of gonad. Lumen with synaptic and post-synaptic spermatocytes, occasionally with a few spermatids.

Predominantly oogonia and synaptic oocytes up to 25μ in females. Connective tissue interspersed between follicles. Phagocytes often associated with connective tissue (Fig. 18B and Fig. 19D,E).

III Maturing I (Differentiated). Egg or early sperm development for the first time. Gonad slightly larger but remaining flat and angular. Clear differentiation into testis (whitish) and ovary (light orange). Loop of alimentary canal still visible. Follicles small and sparse; substance of gonad loose.

Numerous synaptic and post-synaptic polygonal spermatocytes and

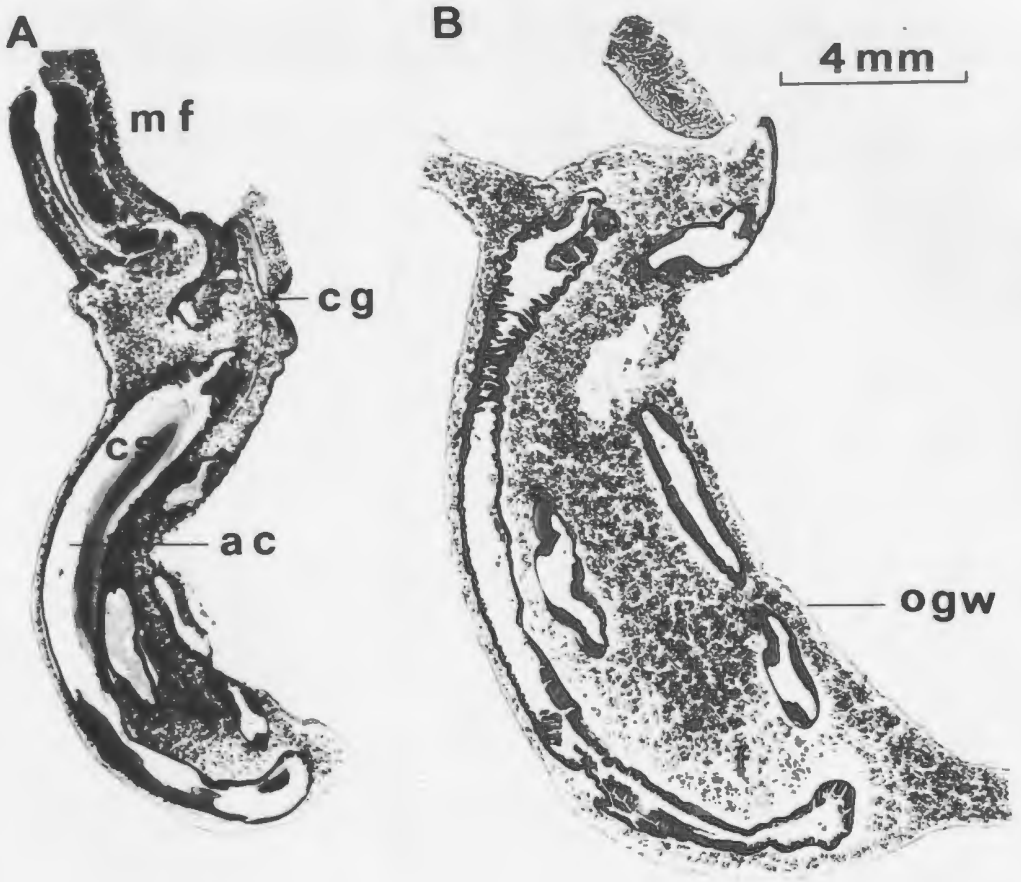


Fig. 18. *P. magellanicus*, L.S. of gonad; A. Differentiated (Immature); B. Developing (Virgin).

(mf. Muscular foot; cg. Ciliated gonoduct; cs. Crystalline style; ac. Alimentary canal; ogw. Outer wall of gonad).

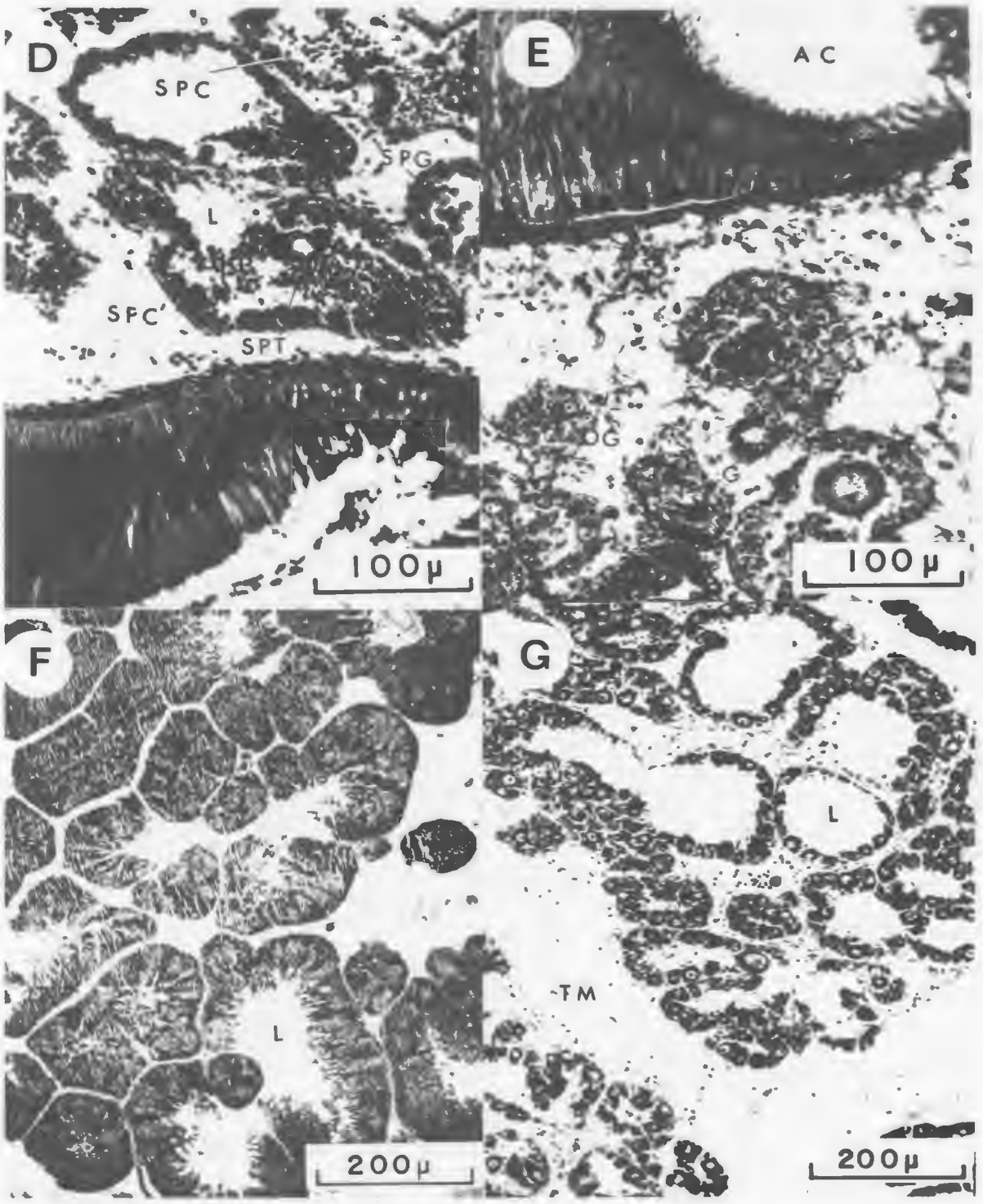


Fig. 19. Description of gonad stages (Cont'd.)

D. Developing (Virgin) male; E. Developing (Virgin) female

F. Differentiated male (Maturing I); G. Differentiated female (Maturing

(SPG. Spermatogonia; SPC. Primary spermatocytes, SPC'. Secondary spermatocytes;

SPT. Spermatids; AC. Alimentary canal; OG. Oogonia; G. Ciliated gonoduct;

L. Lumen; TM. Transverse muscle fibres*).

*Unfortunately these are not visible here as they have been lost in copying. See, however, Fig. 31B.

		some spermatids (1.5-2.0μ) resulting in a multi-layered lining of follicles; some spermatozoa appear at the centre of the lumen. Reduction in connective tissue, usually restricted to below gonad epithelium, between follicles, around the digestive canal and ciliated gonoducts. Synaptic oocytes on follicle wall; some oogonia; oocytes often stalked with granular cytoplasm. Much less connective tissue within the matrix containing the reproductive elements (Fig. 19F,G).
IV	Maturing IA (Recovering).	Gonad larger, depending on size of scallop. First recognizable stage of recovery after spawning. Flabby, containing much free water; assuming characteristic brighter colours (testis, pale white; ovary, light orange). Follicles larger and denser; loop of alimentary canal visible, sometimes protruding from the gonad surface.

Spent gonad of last spawning now with proliferation of oocytes or spermatocytes.

Many spermatogonia and spermatocytes still present near follicle wall; more spermatozoa.

Lumina filling with growing oocytes 25-60μ, some oogonia and synaptic oocytes may be present. Genital ducts losing circular configuration (Fig. 20H,I).

V Maturing II (Filling). Gonad larger and thicker but somewhat flabby because of water within the gonad. Testis white, ovary light red; follicles clearly visible. Alimentary canal not usually seen; distinct visceral arteries.

Radially arranged spermatozoa in male follicles; lumen of females contain half-grown oocytes, many of them attached to the follicle wall by slender peduncles. A thin vitelline membrane may be seen around some oocytes. Few follicle walls still contain primary germ cells. Little connective tissue (Fig. 20J,K).

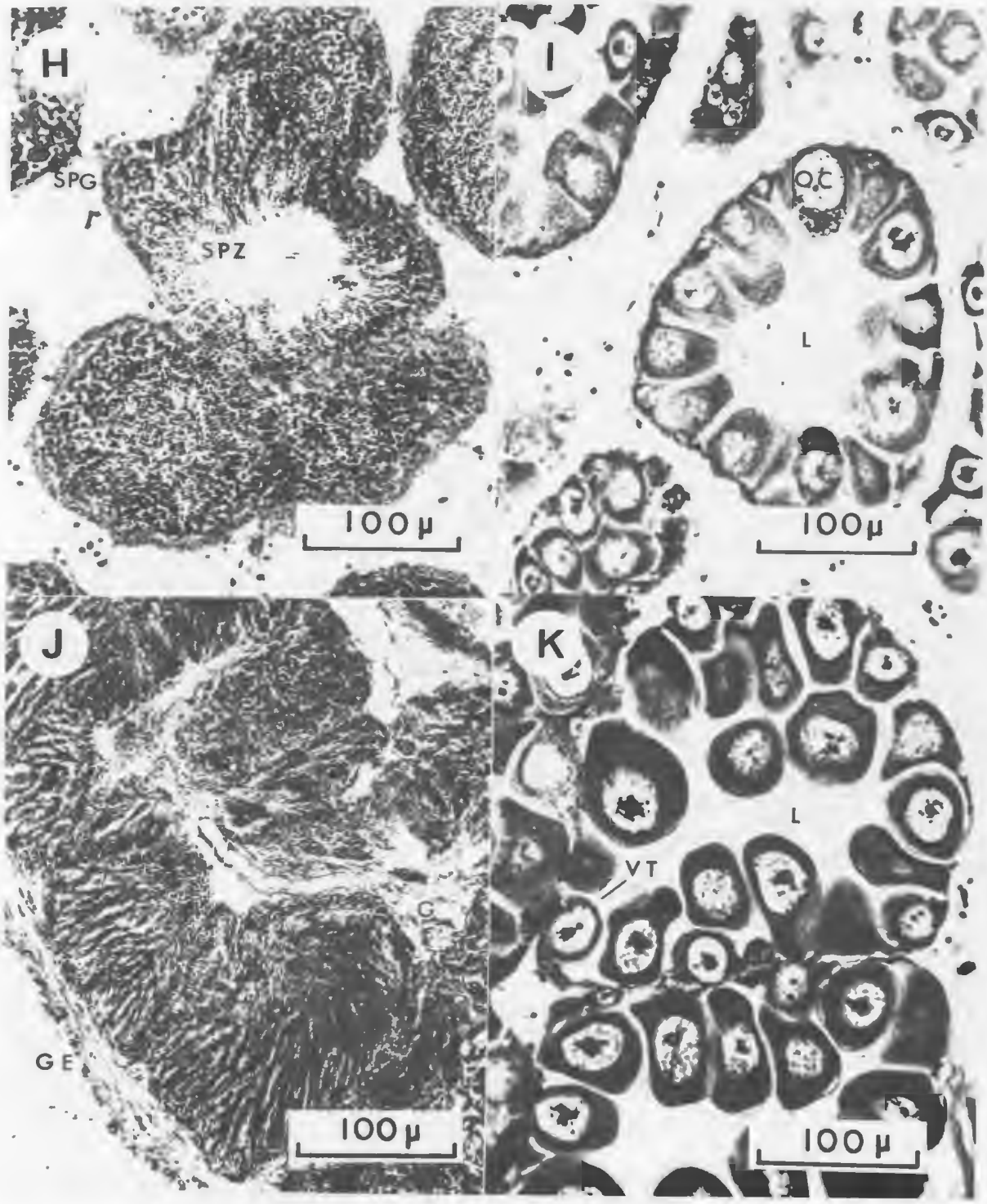


Fig. 20. Description of gonad stages (Cont'd.)

H. Recovering male (Maturing IA)

I. Recovering female (Maturing IA)

J. Filling male (Maturing II)

K. Filling female (Maturing II)

(SPG. Spermatogonia; SPZ. Spermatozoa; OC. Oocyte; L. Lumen of follicle; G. Ciliated gonoduct; VT. Vitelline membrane).

VI Maturing III (Half-full). Gonad again larger and thicker, firmer and becoming rounded in outline, containing little free water. Distal end of gonad pointed. Follicles packed and gonads appear granular; testis creamy-white and ovary brick-red. Alimentary canal invisible except for portions of the loop lying immediately below the gonad epithelium; occasionally the digestive loop causes localized bulging of gonad wall. Visceral arteries becoming prominent within gonad.

Lumina becoming packed with spermatozoa or fully grown oocytes 60-80μ with germinal vesicles usually intact; few spermatogonia and spermatocytes in male or oogonia or synaptic oocytes in female. Further reduction in connective tissue (Fig. 21L,M).

VII Mature (Full). Gonad size at its maximum; thick, rounded and plump, containing no free water and rounded to tip. Follicles packed and assume intense colouration; testis cream and ovary brick-red to a

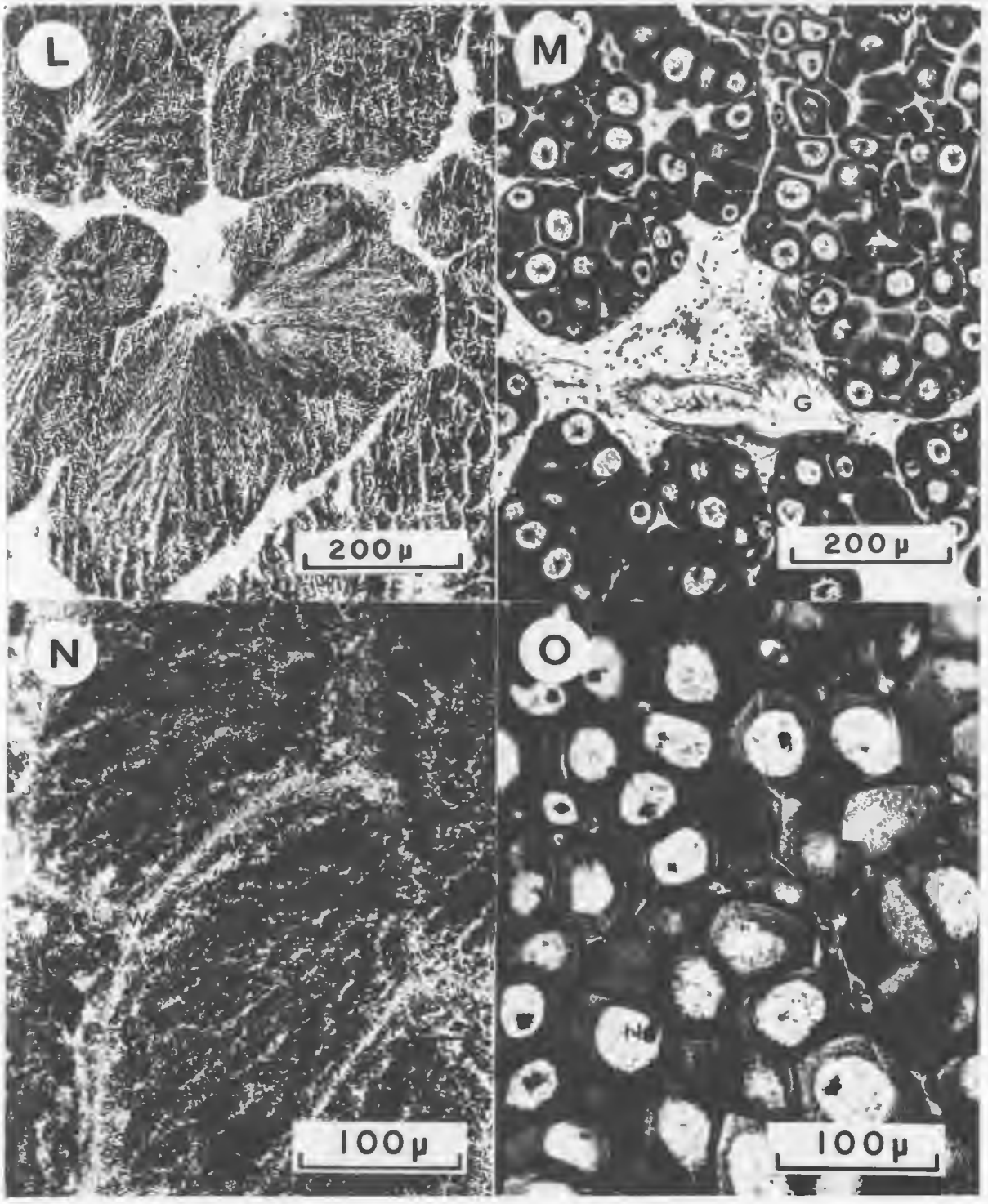


Fig. 21. Description of gonad stages (Cont'd.)

L. Half-full male (Maturing III)

M. Half-full female (Maturing III)

N. Full male (Mature)

O. Full female (Mature)

(G. Ciliated gonoduct; FW. Follicle wall; N. Nucleolus).

bright coral red. Gonad surface smooth, glossy and less granular. Cut surfaces usually gape and expose reproductive elements which now have a thick gelatinous consistency. Alimentary canal indiscernible except when near the gonad wall. Well defined visceral arteries and veins, often pitted. Gonad products may be easily forced into superficial gonoducts with light pressure on gonad wall (Fig. 22A,B).

Primary germ cells at a minimum; male follicles packed with spermatozoa extending to the periphery. Follicle walls extremely thin. Female follicles crowded with polygonal or hexagonal oocytes, whose germinal vesicles show signs of breaking down. Connective tissue restricted to alimentary canal and gonoducts which appear flattened. In fresh smears spermatozoa display various degrees of motility. Mature oocytes become rounded on contact with water (Fig. 21N,O).

VIII Spawning (Initial and partially spent). Gonads retain differentiation. Tissue becoming dull, angular and flabby depending on the number of follicles emptied (Fig. 22C,D). During spawning peak the kidneys are often gorged with sex products. Gonad outline collapses if pierced and gonad shrivels up losing the free water within. Visceral mass and gills of females sometimes tinged orange in spawning females. Gonads of spawning males frequently showing patches of translucent tissue and regions of comparatively opaque tissue indicating empty and full follicles respectively. Tip of gonad becoming progressively more pointed as spawning proceeds.

Regions containing unspawned follicles contain ripe germ cells and are in stage VII of development. Follicles at varying degrees of spawning are crowded by phagocytes. In some sections ova or sperm may be seen in ciliated ducts (Fig. 29C). In fresh smears sperm are very active (Fig. 23P,Q).

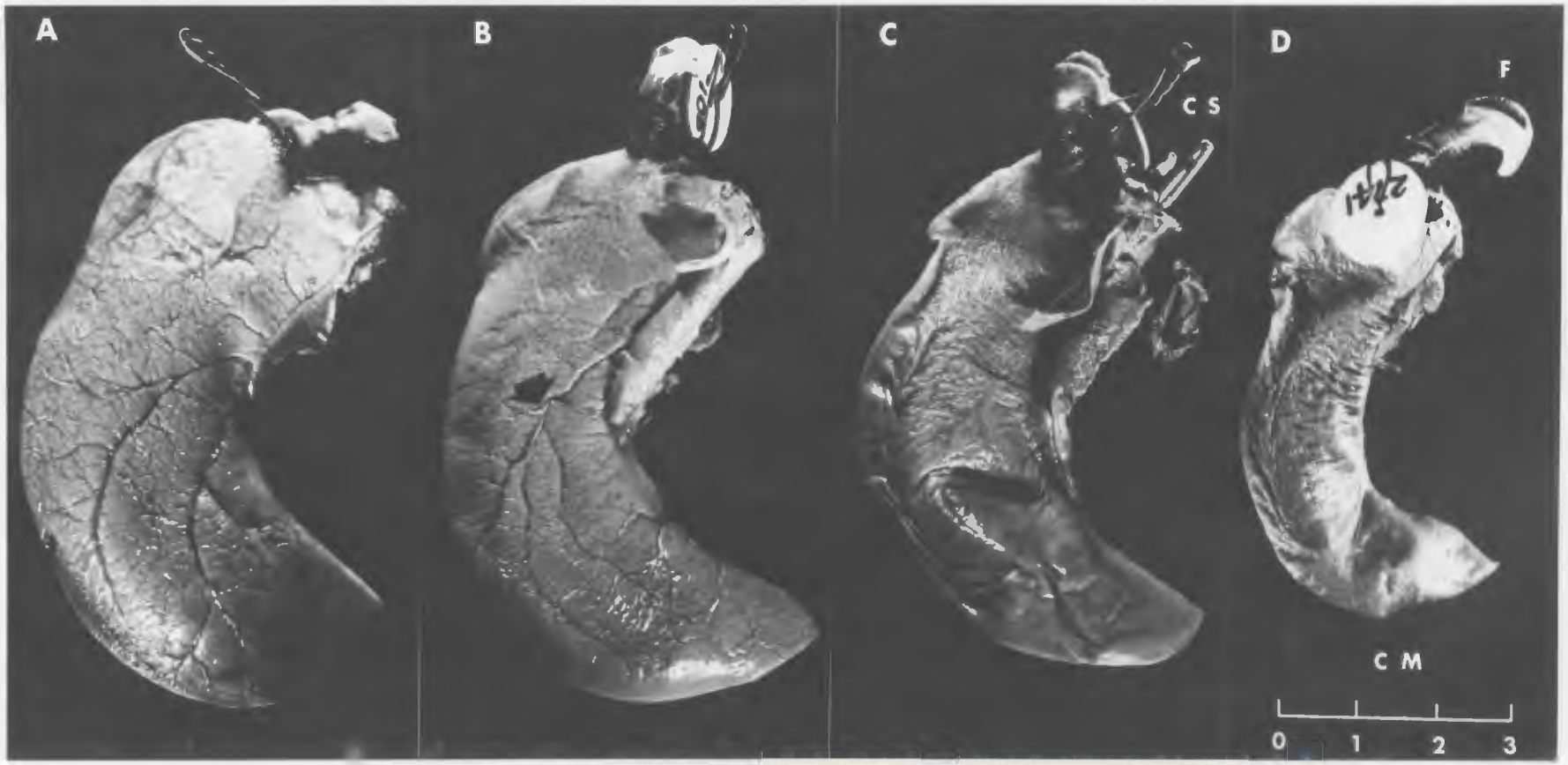
Fig. 22. Description of gonad stages (Cont'd.). Macroscopic appearance of female gonads.

A. Full (mature) gonad. Note prominent visceral arteries and veins.

B. Gonad products in superficial vessels (arrowed)

C. Spawning or partially spent gonad (cs. Crystalline style)

D. Spent gonad (f. Foot).



IX Spent. Gonad considerably shrunken in volume; generally dull, flaccid and fawn coloured; containing much free water which is discharged on piercing the gonad wall. Visible differentiation into testis and ovary sometimes lost. Unemptied or partially spent follicles stand out in the dull background tissue as specks especially near proximal end of gonad. Visceral arteries and veins no longer visible. Gonad tip becomes pointed (Fig. 22D). Loop of alimentary canal can usually be seen.

Follicles empty retaining few residual germ cells. Both connective tissue and follicles phagocytized. In late stages some re-organization of follicles may be seen and early stages in gametogenesis may be present (Fig. 23R,S).

Monthly changes in gonadal maturity for all ages during the years 1966 and 1967 are summarized in Table 20 (Fig. 24). Maturity stages are also tabulated by sex at each date of collection at roughly weekly intervals (Table 21 and 22). This allowed a more precise identification of

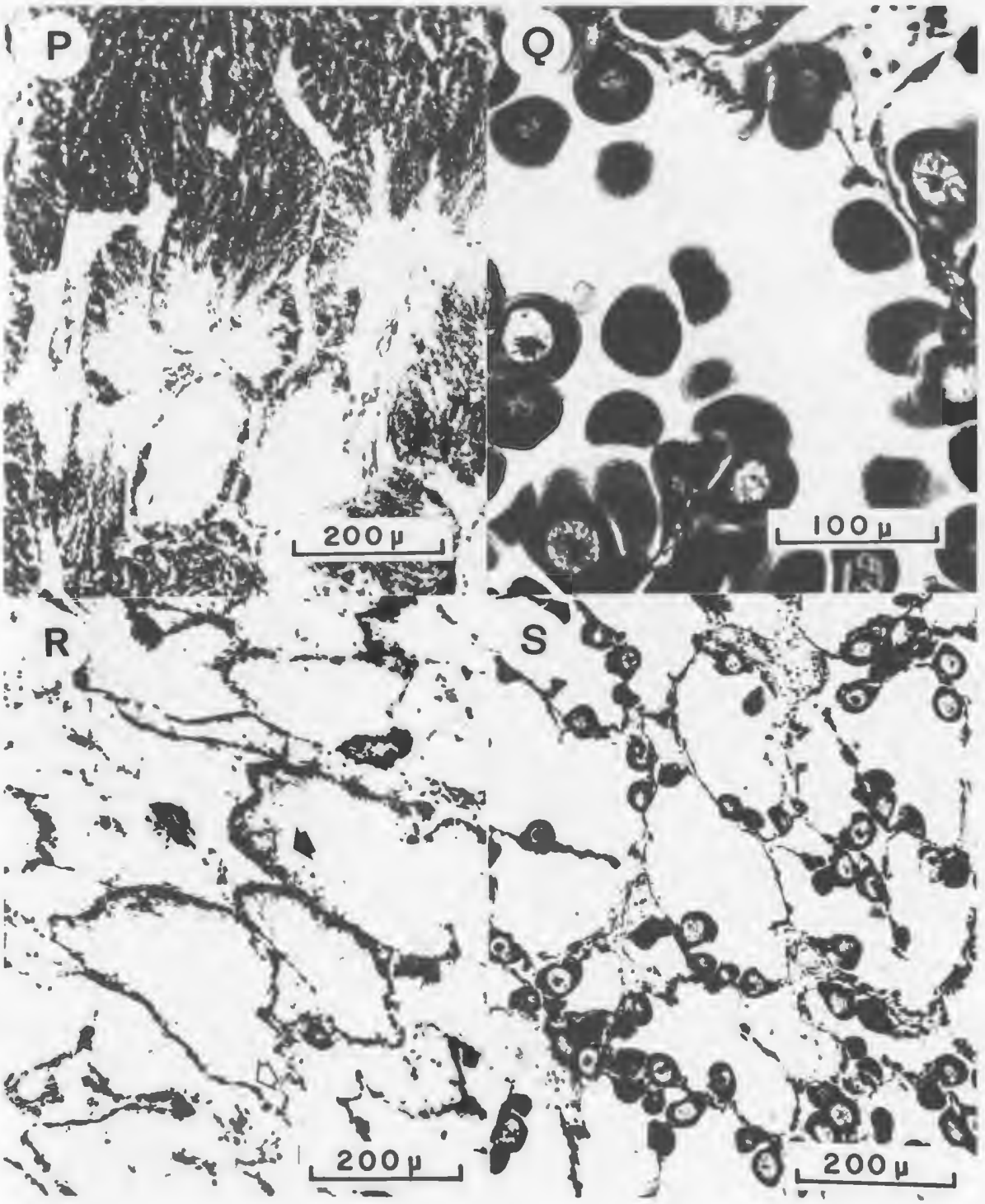


Fig. 23. Description of gonad stages (Cont'd.)

P. Spawning male (Partially spent)

Q. Spawning female (Partially spent)

R. Spent male with residual spermatozoa (solid arrow) and early gametogenetic activity on follicle wall (open arrow)

S. Spent female with residual oocytes.

Table 20. Monthly percentages of the various stages of gonadal development and spawning in *P. magellanicus* in Port au Port Bay, Newfoundland during 1966 and 1967.

Year	Month	No. of scallops examined	Gonad stages									
			0	I	II	III	IV	V	VI	VII	VIII	IX
1966	May	219	0.5	-	0.9	0.9	0.5	1.4	94.5	1.4	-	-
	June	329	-	-	0.6	4.0	1.2	1.5	86.0	0.6	6.0	-
	July	346	-	0.3	4.3	5.2	-	-	88.7	-	1.5	-
	August	563	-	-	2.1	3.7	-	21.3	69.3	3.6	-	-
	September	367	-	-	3.3	1.6	-	-	-	8.2	38.7	48.2
	October	116	-	-	-	0.9	-	-	-	-	58.6	40.5
	November	119	-	-	-	0.8	-	-	-	-	8.4	90.8
	TOTAL	2059										
1967	May	208	-	-	1.4	1.0	1.9	59.1	36.5	0.9	-	-
	June	332	-	-	-	0.3	0.9	-	10.8	52.4	36.6	0.9
	July	116	-	-	1.7	1.7	-	-	7.8	88.8	-	-
	August	109	-	-	-	-	-	-	0.9	3.7	80.7	14.7
	September	17	-	-	-	-	-	-	-	11.7	17.7	70.6
	October	166	-	-	-	-	1.2	-	-	-	6.2	92.8
	TOTAL	948										

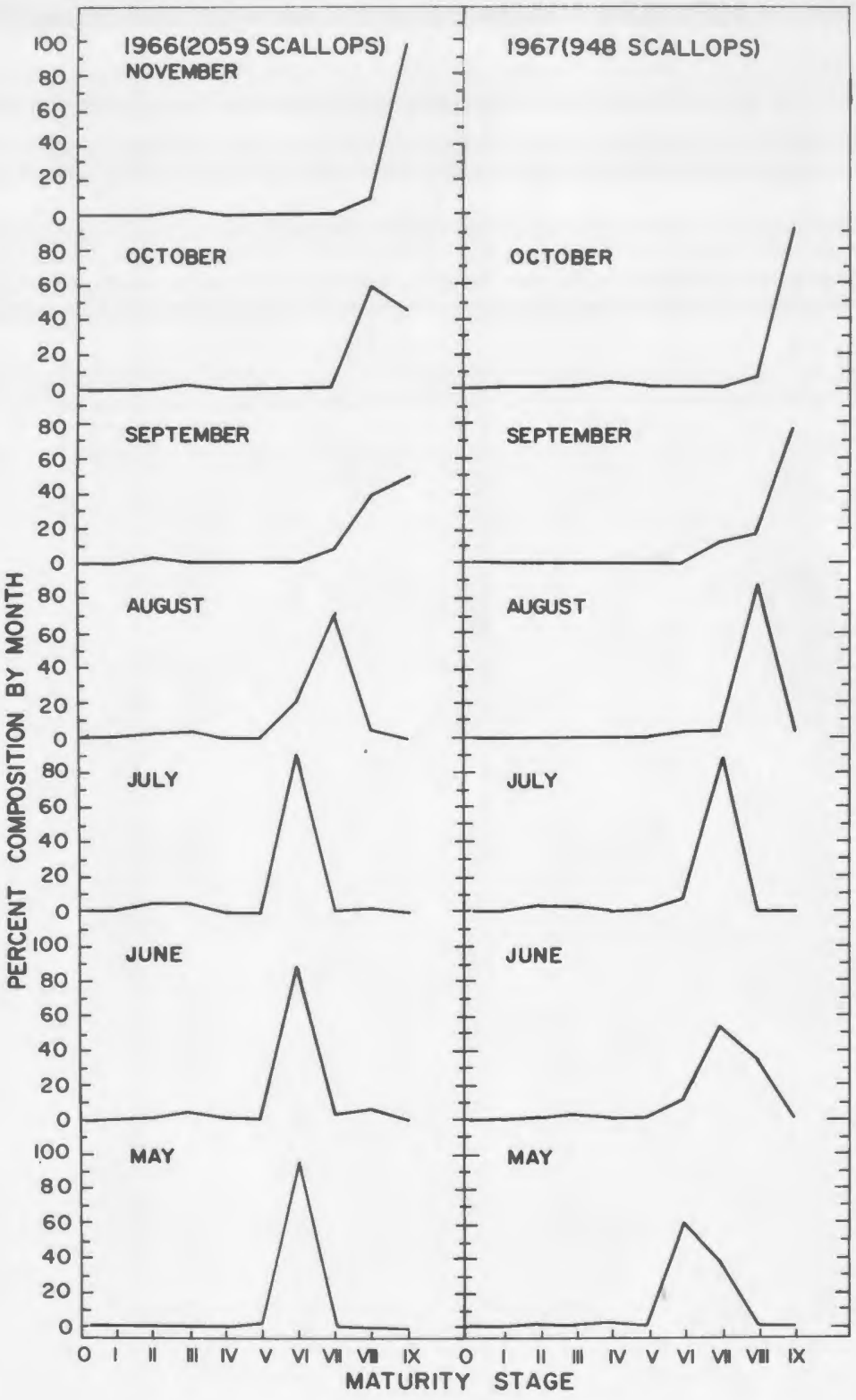


Fig. 24. Monthly changes in gonadal maturity of the giant scallop in Port au Port Bay, Newfoundland during the years 1966 and 1967.

Table 21. Maturity stages by sex at each date of collection of *P. magellanicus* from Port au Port Bay, Newfoundland (1966 data).

1966 Sample No.	Date	Sex	Frequency of maturity stages 0	I	II	III	IV	V	VI	VII	VIII	IX	Totals
1	May 17	M	1		1			1	11	1			15
		F						2	13	1			16
2	May 23	M				1			29				30
		F							48				48
3	May 31	M			1		1		52	1			55
		F				1			54				55
4	June 9	M						2	10				12
		F						2	14				16
5	June 13	M			1	1	2		40				44
		F			1		1	1	43	1			47
6	June 20	M				5			47	1			53
		F				2			47				49
7	June 27	M				4	1		52		6		63
		F				1			44				45
8	July 4	M			1	1			58				60
		F							47		4		51
9	July 12	M			3	2			54				59
		F							59				59
11	July 27	M			8	13			44		1		66
		F			3	2			45				50
12	August 1	M			3	3			50				56
		F				1			59		1		61

Cont'd.

Table 21 Cont'd.

1966 Sample No.	Date	Sex	Frequency of maturity stages 0	I	II	III	IV	V	VI	VII	VIII	IX	Totals
13	August 8	M			1	2			1	17			21
		F							5	14	1		20
14	August 11	M			2	4				65	1		72
		F								56	4		60
15	August 15	M			1	2			1	44	3		51
		F			1					53	2		56
16	August 19	M				2			1	20	2		25
		F								26			26
17	August 22	M			3	5				38	2		48
		F							3	33	3		39
18	August 30	M			1	2				11	1		15
		F								12			12
19	September 5	M			5	3				12	24	7	51
		F								17	24	11	52
20	September 13	M			2					1	25	44	72
		F			2						24	39	65
21	September 21	M			2	2					27	32	63
		F			1	1					17	44	63
22	October 24	M			1	1					32	31	65
		F									35	16	51
23	November 31	M				1					5	74	80
		F									5	34	39

Table 22. Maturity stages by sex at each date of collection of *P. magellanicus* from Port au Port Bay, Newfoundland (1967 data).

1967 Sample No.	Date	Sex	Frequency of maturity stages										
			0	I	II	III	IV	V	VI	VII	VIII	IX	Totals
24	May 24	M							35	10			45
		F				1	1		57	6			65
25	May 25	M				1	2		8	30			41
		F					1		23	30			54
26	June 28	M				1	1		13	83	45	2	145
		F					2		23	91	70	1	187
27	July 27	M				2			5	40			47
		F			1				4	63			68
28	August 31	M								2	49	9	60
		F							1	2	39	7	49
29	September 26	M									1	7	8
		F								2	2	5	9
30	October 26	M									4	83	87
		F					2				8	69	79

the exact spawning time in the bay. Finally monthly changes in gonad weight accompanying the breeding cycle in 1966 are shown in Table 23 and depicted graphically in Fig. 25.

In Port au Port Bay scallops first spawn following the deposition of what has been defined here as the first growth ring. Gonads were well advanced by early June and were usually in stage VI or VII of development. There was a small spring or early summer spawning in some individuals

Table 23. Monthly variation in gonad weights in *P. magellanicus* from the Boswarlos bed, Port au Port Bay, Newfoundland for 1981 specimens examined.

Month	Sex	Gonad weight at age (gm)														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
May	Male	0.1	1.1	2.8	9.0	11.6	19.1	17.1	17.2	20.3	21.8	25.9	21.8	23.5	21.5	-
	Female	-	1.3	1.6	4.7	7.4	11.0	15.3	16.0	16.6	18.8	19.8	23.0	-	-	-
June	Male	0.1	0.5	1.8	4.8	8.0	13.0	14.2	15.4	16.8	18.4	19.5	22.3	-	-	-
	Female	-	0.4	1.6	-	7.0	10.9	11.3	11.6	15.8	15.7	17.1	19.4	-	-	-
July	Male	0.0	0.4	1.6	4.1	7.8	11.3	12.7	16.7	14.6	16.1	16.4	19.2	19.1	15.3	-
	Female	0.1	0.4	1.5	2.9	6.5	8.7	9.1	9.4	13.5	12.7	14.2	17.8	-	-	16.9
August	Male	0.1	0.5	2.2	6.7	9.2	11.4	13.0	15.5	16.1	17.8	17.2	20.3	21.2	-	17.5
	Female	0.1	0.7	2.2	5.2	8.5	11.2	13.1	13.1	13.8	17.5	17.2	20.1	22.1	16.8	-
September	Male	0.2	1.0	2.0	4.9	7.9	8.1	14.8	10.2	12.5	13.4	14.0	17.5	17.6	-	-
	Female	0.1	1.1	1.9	4.4	7.3	9.0	9.3	9.0	10.7	13.6	14.1	12.3	17.2	11.0	13.0
October	Male	0.0	0.2	1.4	2.1	5.9	6.1	6.7	6.5	-	9.6	6.3	13.7	-	-	-
	Female	-	0.1	1.3	2.7	4.1	6.6	7.5	-	6.6	8.5	10.0	10.0	12.3	-	-
November	Male	0.1	0.9	1.9	4.0	7.1	9.2	5.7	11.0	10.0	10.8	13.4	-	-	-	-
	Female	-	-	2.1	3.8	5.9	7.6	5.8	5.5	12.0	9.6	10.3	-	-	9.7	-

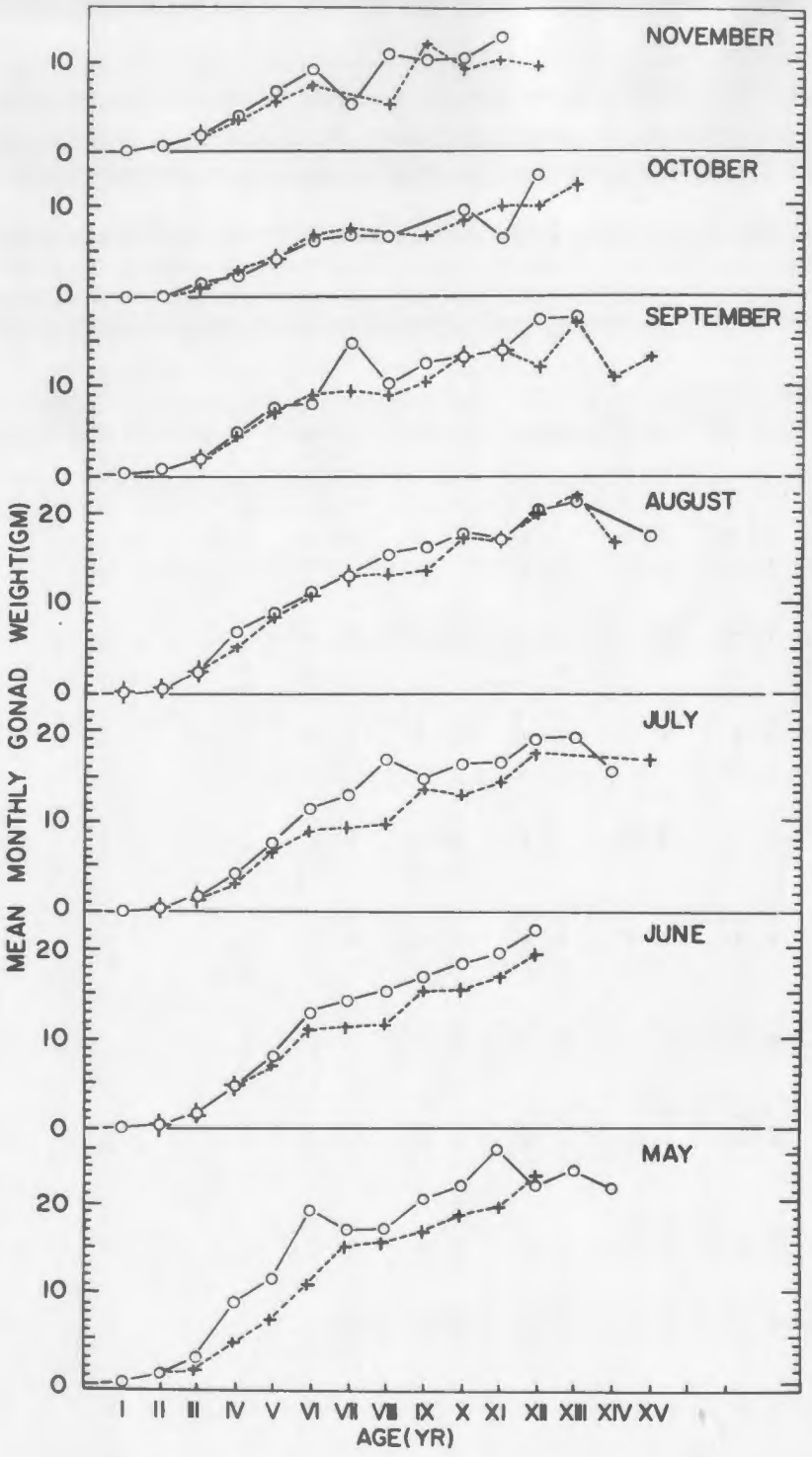


Fig. 25. Changes in monthly gonad weights of the scallop accompanying the breeding cycle in Port au Port Bay during 1966 (o Males, + Females).

followed by a major spawning in the fall (September to October). The initial spawning in June was minor and only a few individuals seemed to take part. Fall spawning was more complete and the majority of scallops appeared to shed their reproductive products at this time. Various states or degrees of repletion may be seen throughout the spawning period. Spawning in both years was protracted and lasted from about late August to October. The exact time and duration of spawning was different during the two years studied. By late November spawning appeared to be completed in most of the individuals examined. Some gonads even at this time of the year were still replete. Wide variations in the condition of the follicles were encountered not only in different individuals but for different follicles of the same individuals collected at the same time and place. Photomicrographs of these variations are shown for the months May to November in Fig. 26-32.

In June 1966 only 6 out of 329 scallops examined were either spawning or in a partially spent condition. The major spawning began during the first week of September when the water temperature on the grounds varied between 4.2 and 16.1°C and was falling (Fig. 33). On September 5, 47% of the scallops examined were spawning and 18% were spent out of a total of 104 examined. All adult scallops except one examined on September 13 were either spawning (36%) or in a spent condition (61%). By the end of November 108 out of a total of 119 (91%) were completely spent. The rest of the gonads continued to show some evidence of spawning.

In June 1967, 115 from a total of 332 (34.6%) scallops examined demonstrated some spawning activity. This is a higher percentage than for the

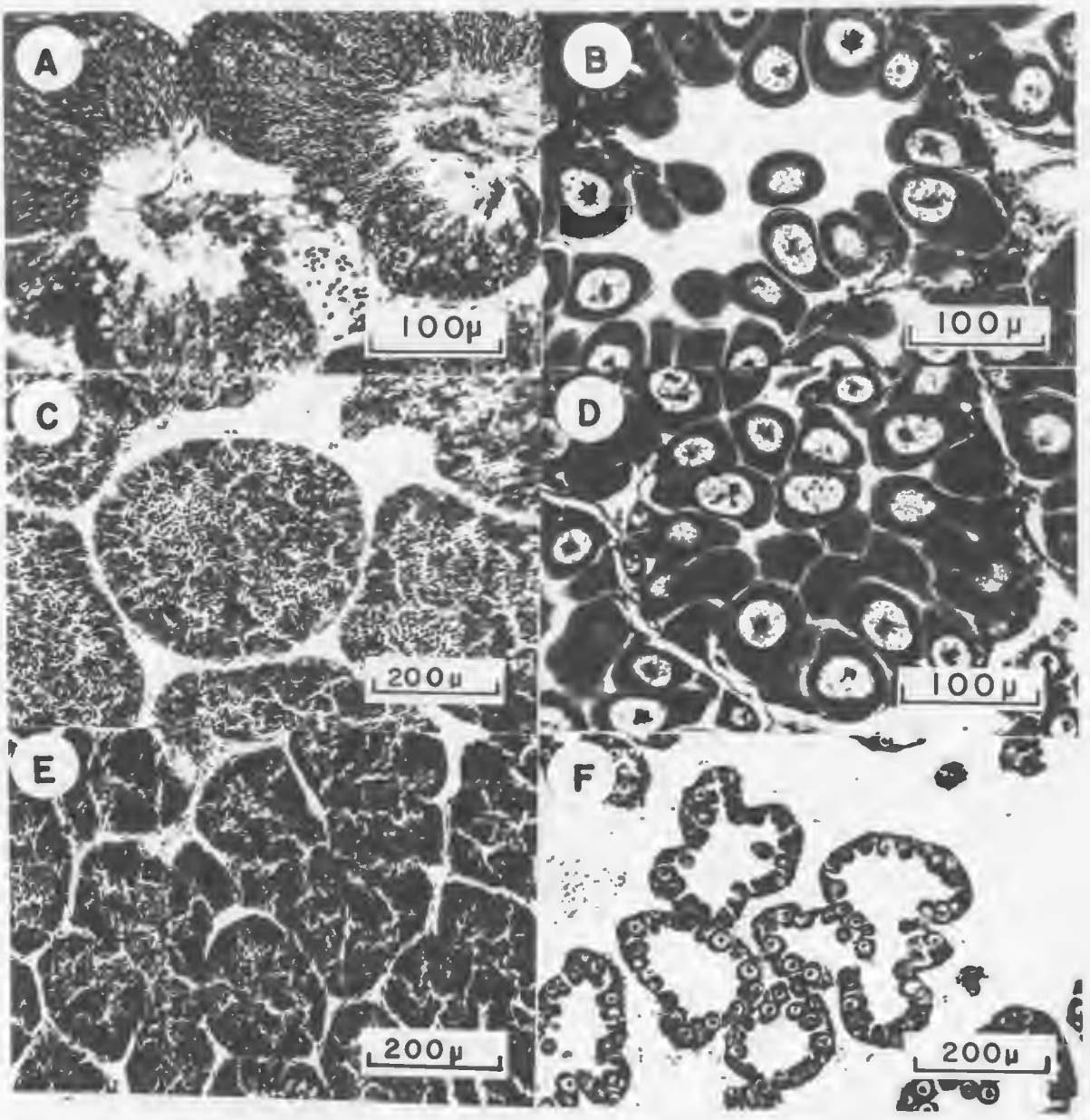


Fig. 26. A-F. Photomicrographs showing variation in follicle condition in May 1966 in different individuals collected at the same time and place.

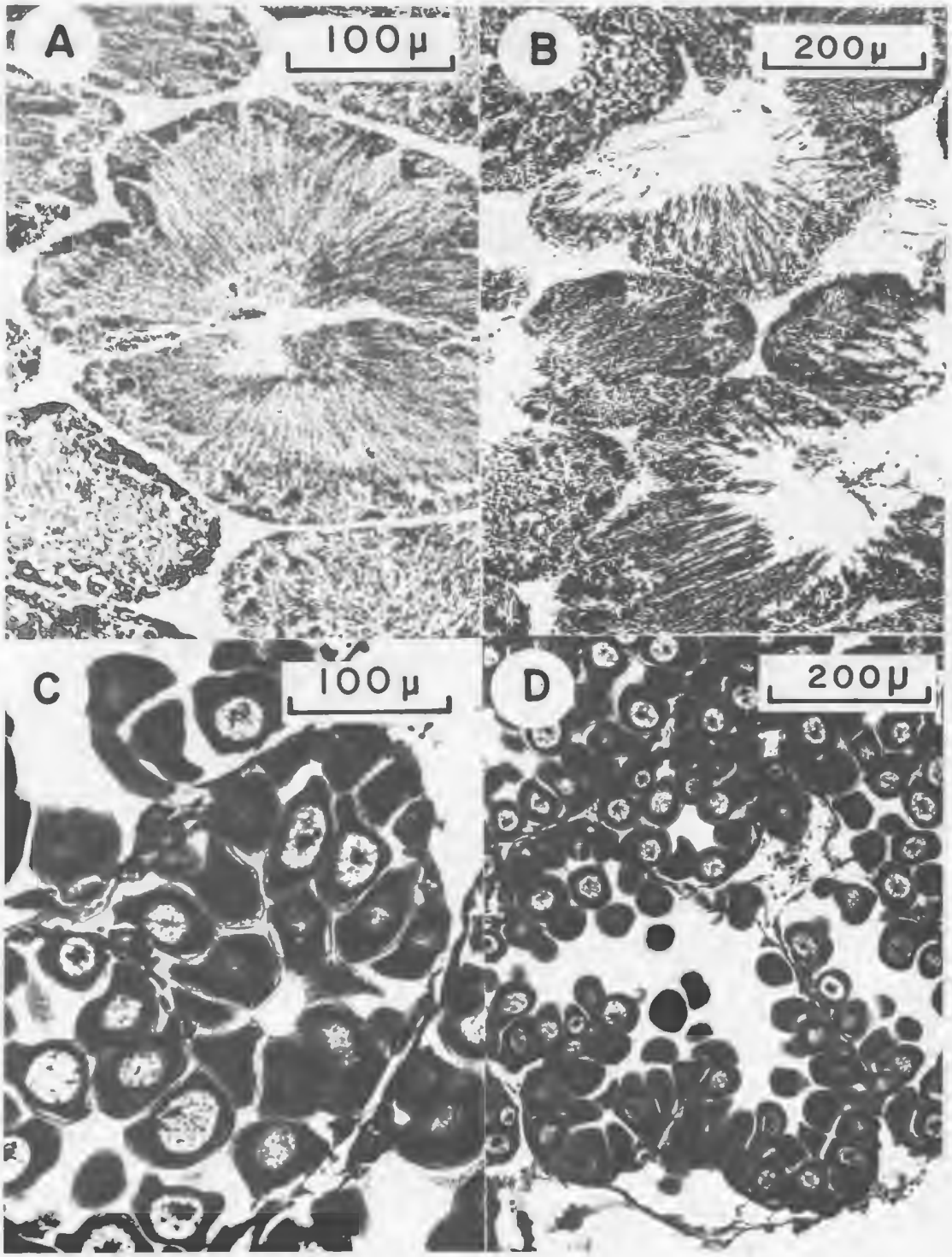


Fig. 27. A-D. Variations in follicle condition in June 1966.

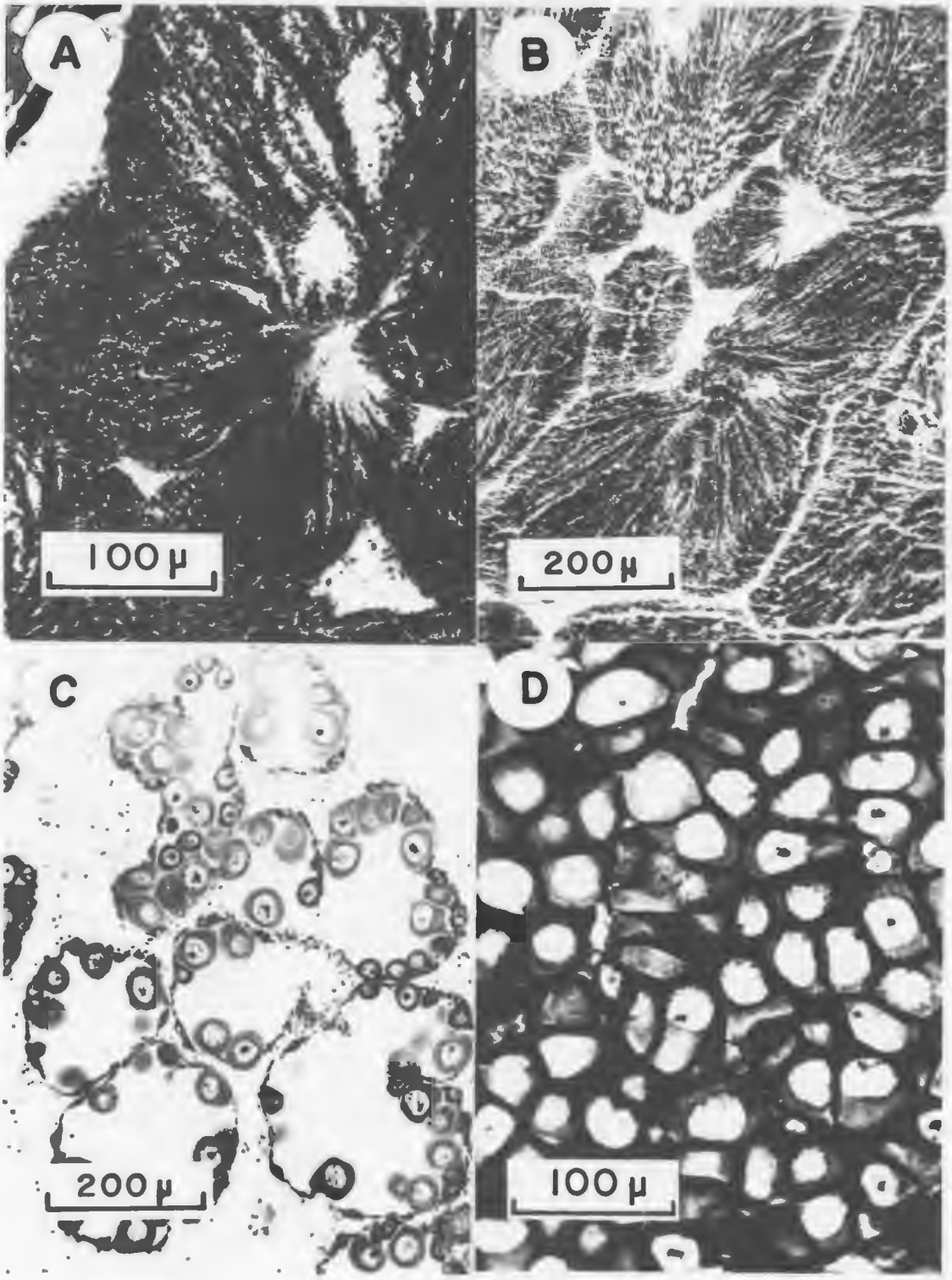


Fig. 28. A-D. Variations in follicle condition in July 1966.

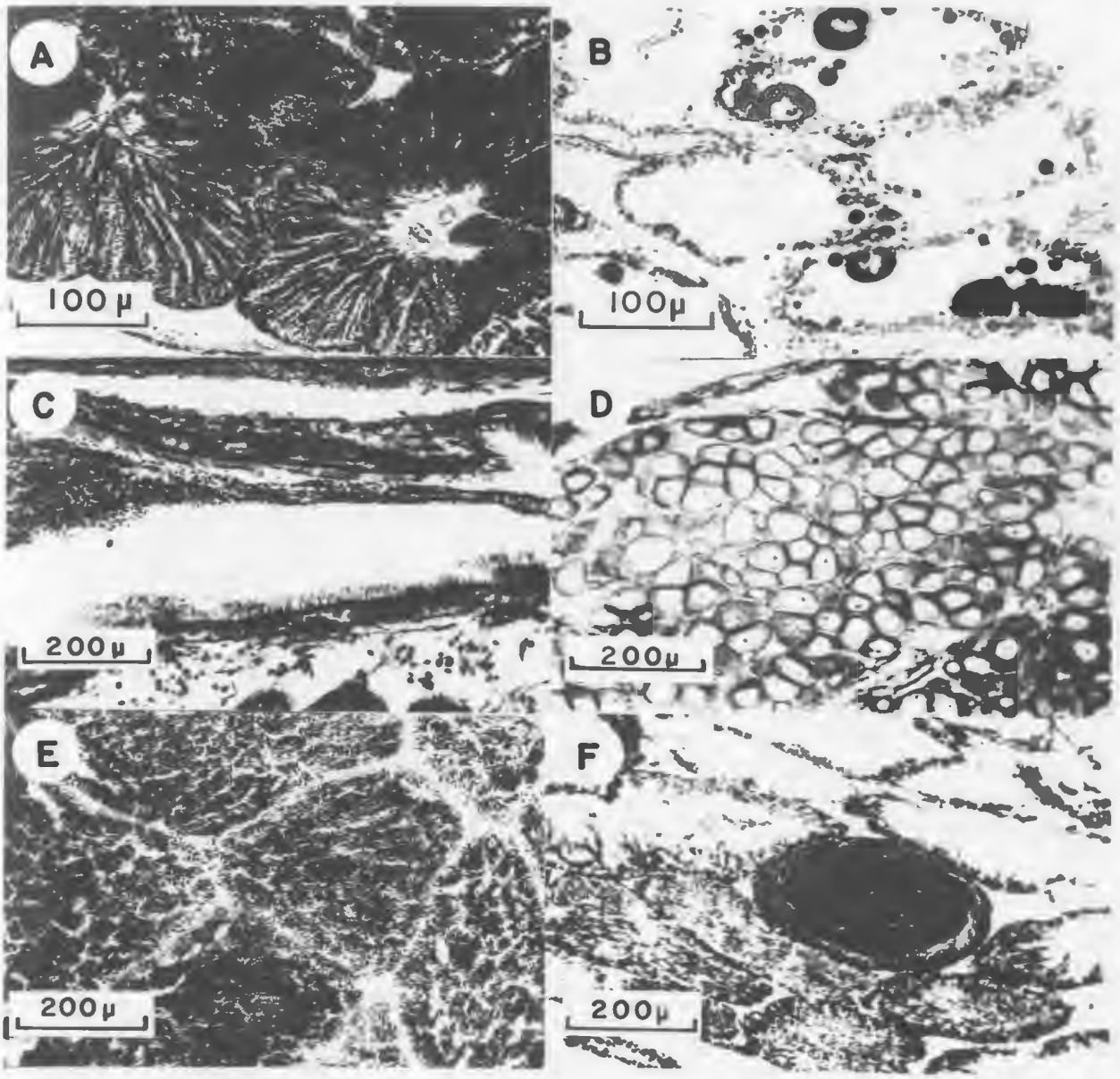


Fig. 29. A-F. Variations in follicle condition in August 1966. (B) Residual oocytes undergoing cytolysis; (C) Spermatozoa in ciliated gonoduct of a spawning male.

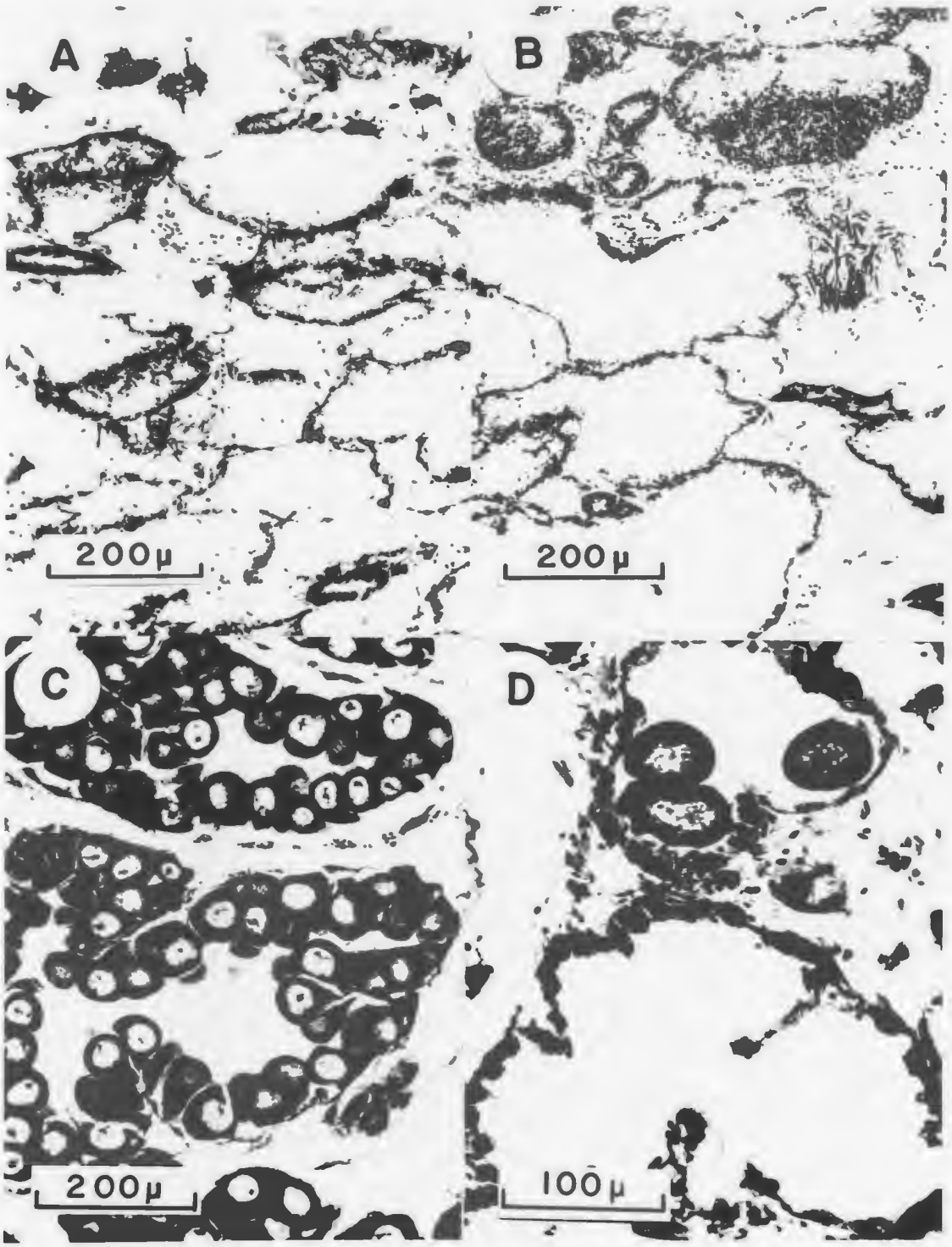


Fig. 30. A-D. Variations in follicle condition in September 1966.

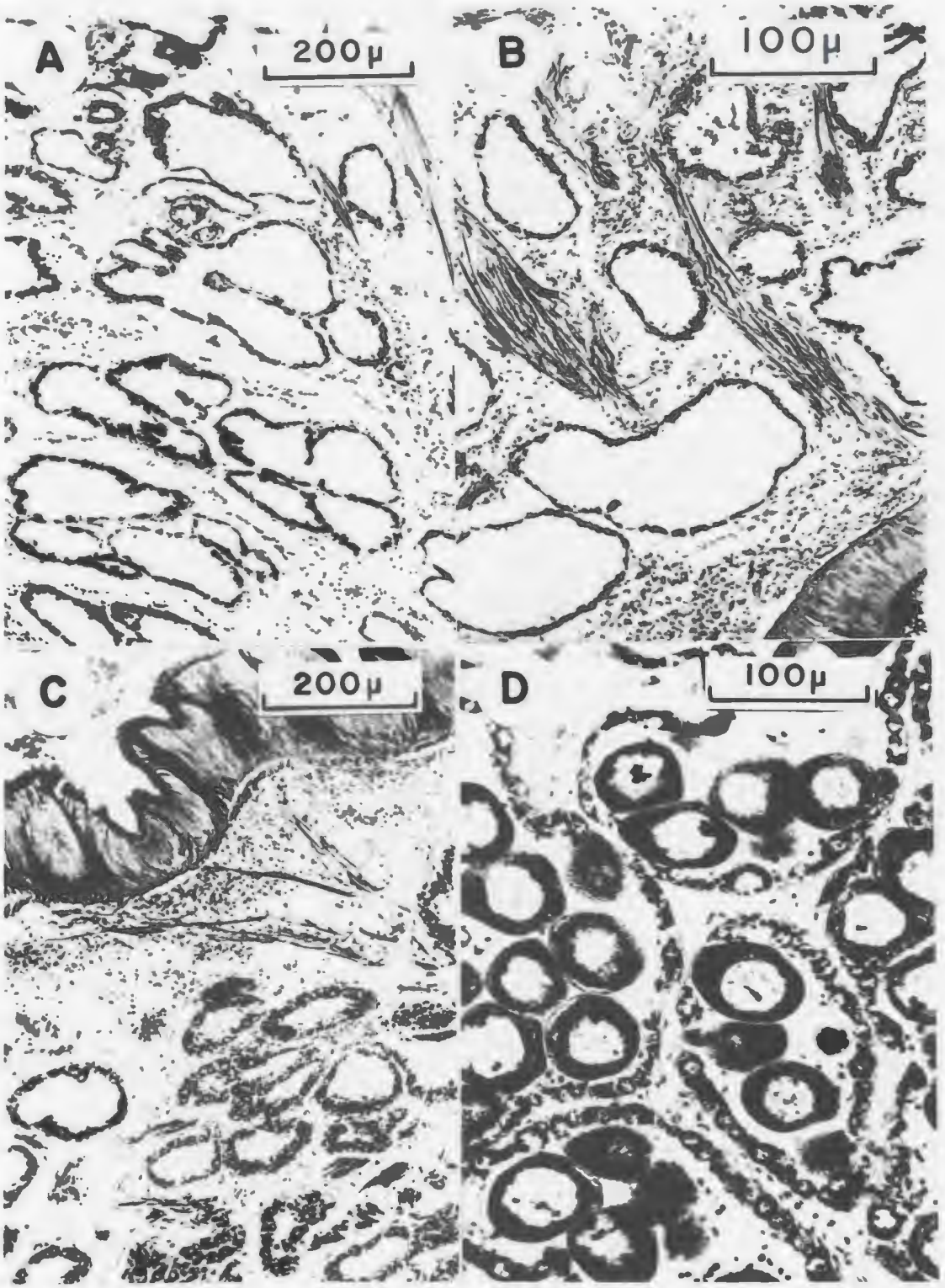


Fig. 31. A-D. Variations in follicle condition in October 1966.

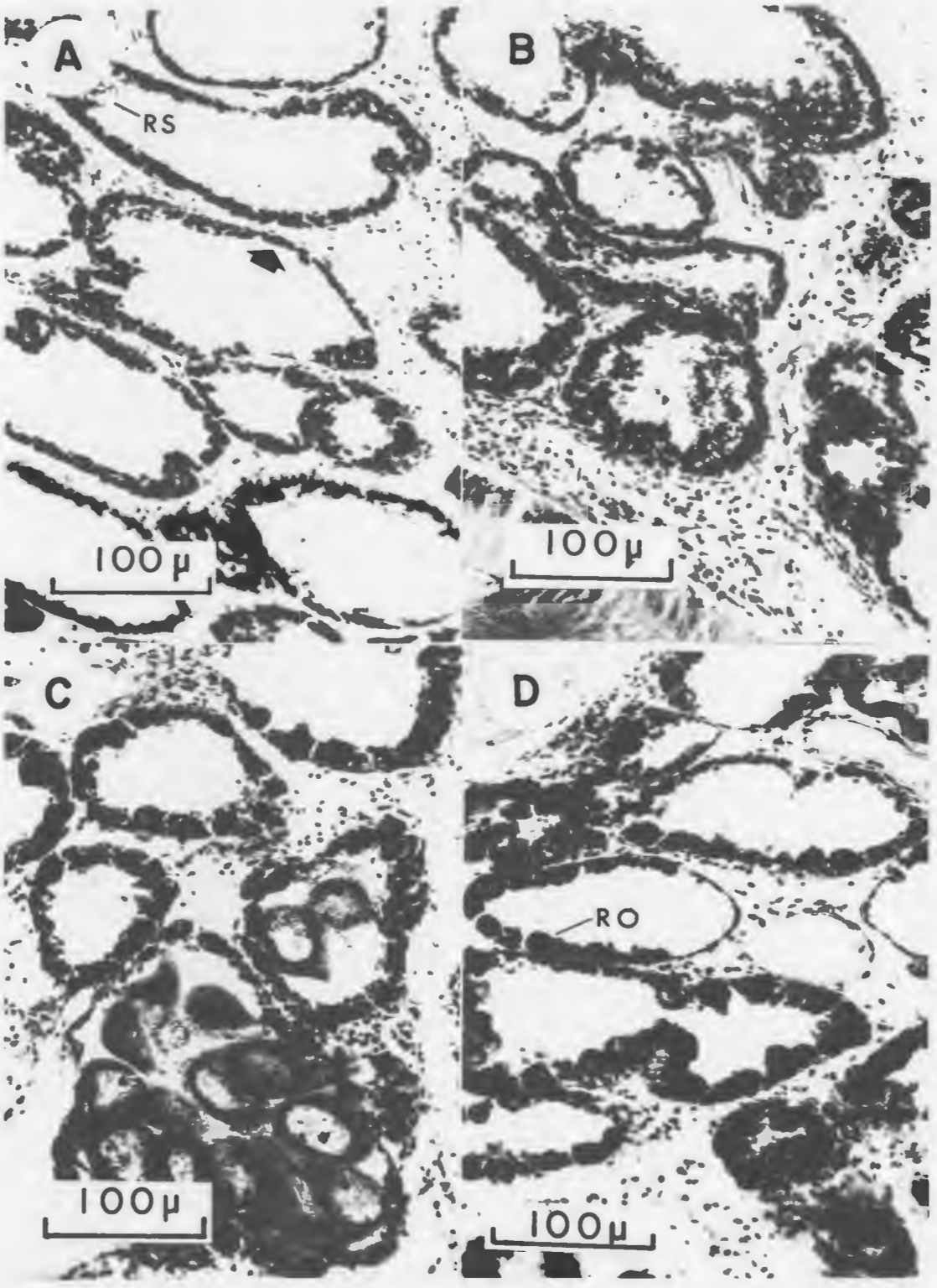


Fig. 32. A-D. Variations in follicle condition in November 1966. (RO. Residual oocytes; RS. Residual spermatozoa. Arrow in (A) indicates resumption of gametogenetic activity.)

same period the previous year. The temperature on the grounds on June 26 was 8.6°C and rising (Fig. 33). No spawning activity was encountered in July. At the end of August spawning was well underway and 88 out of 109 (80.7%) scallops examined on August 31 were spawning. About 93% of the 166 scallops examined during the last week of October were spent, thus completing their spawning phase earlier and in a shorter time than they did in the previous year. Monthly changes in gonadal maturity for the two years are shown in Fig. 24.

The gonad weights display some interesting features during the reproductive cycle (Fig. 25). In general the relationship of gonad weight with age is sigmoid. The testes at any one age are usually heavier than the ovaries. There is a fair amount of scatter of these points in May, but these variations gradually diminish with the ripening of the gonad and is at a minimum in August when about 70% of the gonads are full. Between August and September a considerable reduction in gonad weights at each age has occurred and this continues into October. Accompanying this depression in gonad weights is an increase in the amount of scatter in the points. As expected the period of maximal reduction in gonad weights occurs during peak spawning activity. There is a slight increase in the average gonad weights at each age in November.

Fresh smears of the gonad

All testes except those in stages 0, I and II contain active spermatozoa. The number of active elements increases with reproductive maturity.

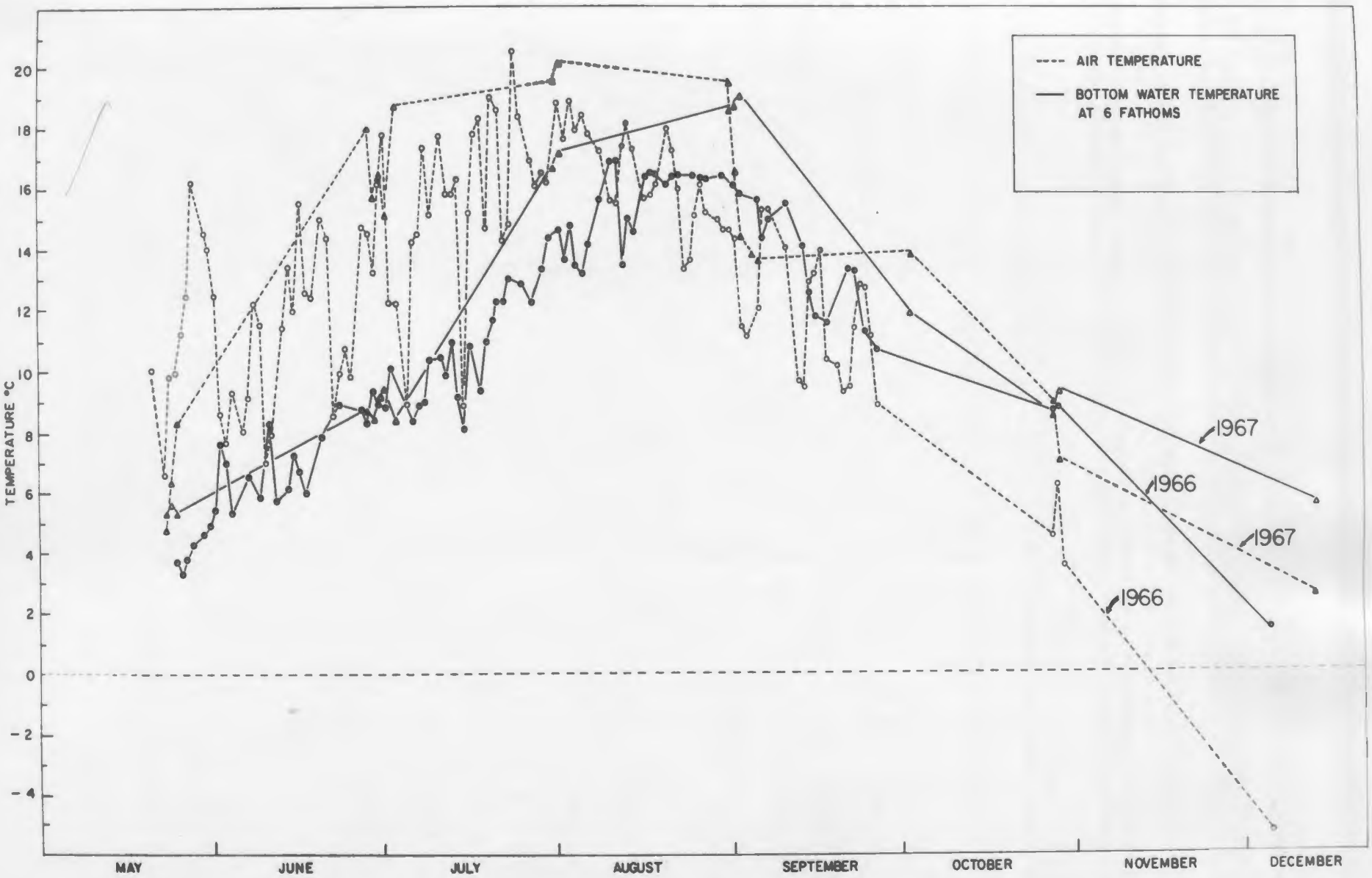


Fig. 33. Daily variations in air and bottom temperatures at 6 fathoms on the Boswarlos bed (May-September 1966) and observed temperatures at each date of collection (September-December 1966 and May-December 1967).

Ovarian smears showed varying numbers of predominantly small oocytes during stages I and II, with increasing number of larger oocytes in stages III (mature, filling) to VII (full). The germinal disc remains intact except in ripe gonads when some of them show signs of breaking down. Ripe eggs assume a round configuration in sea water.

Plankton tows

What is thought to be the prodissoconch stage of the giant scallop was found in several tows with a peak between September 10-20 in 1966. Veliger stages were not encountered. Time did not permit positive identification of the prodissoconch stage from plankton samples. Consequently this section has been omitted here.

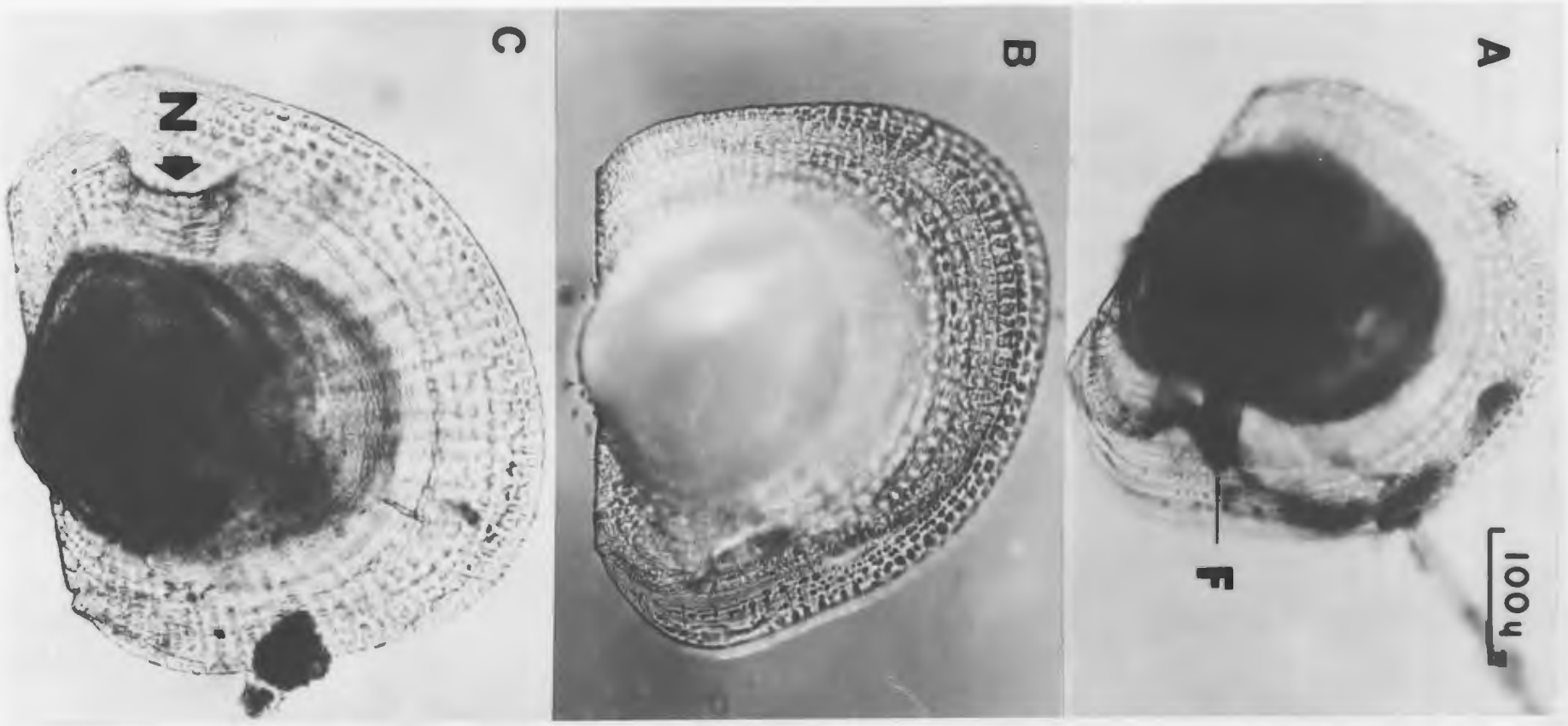
Juvenile scallops

Of the materials used, wooden buoys and scallop shells were found to be most suited to the settlement of young scallops. Large numbers of small scallops at the dissoconch stage of development were found attached to both these substrates. They ranged in size from about 0.3 to 2.5 mm (dorso-ventral axis). The early post-larval scallops possess a small foot which may be seen as a finger-like projection within the thin shell (Fig. 34A). Although plications were not observed on these larval shells they had a fine ornamentation (Fig. 34B). Most of the scallops observed had already developed a well developed byssal notch (Fig. 34C). Dissoconch stages were also found attached by fine byssus threads to a red alga, *Rhodermela conferroides*, growing on wooden buoys (Fig. 35). Attached juvenile scallops were most abundant in late October.

Fig. 34. A. Early post-larval scallop with small foot (F)

B. Dissoconch stage (left valve facing)

C. Dissoconch stage (right valve facing) showing prominent byssal notch (N).



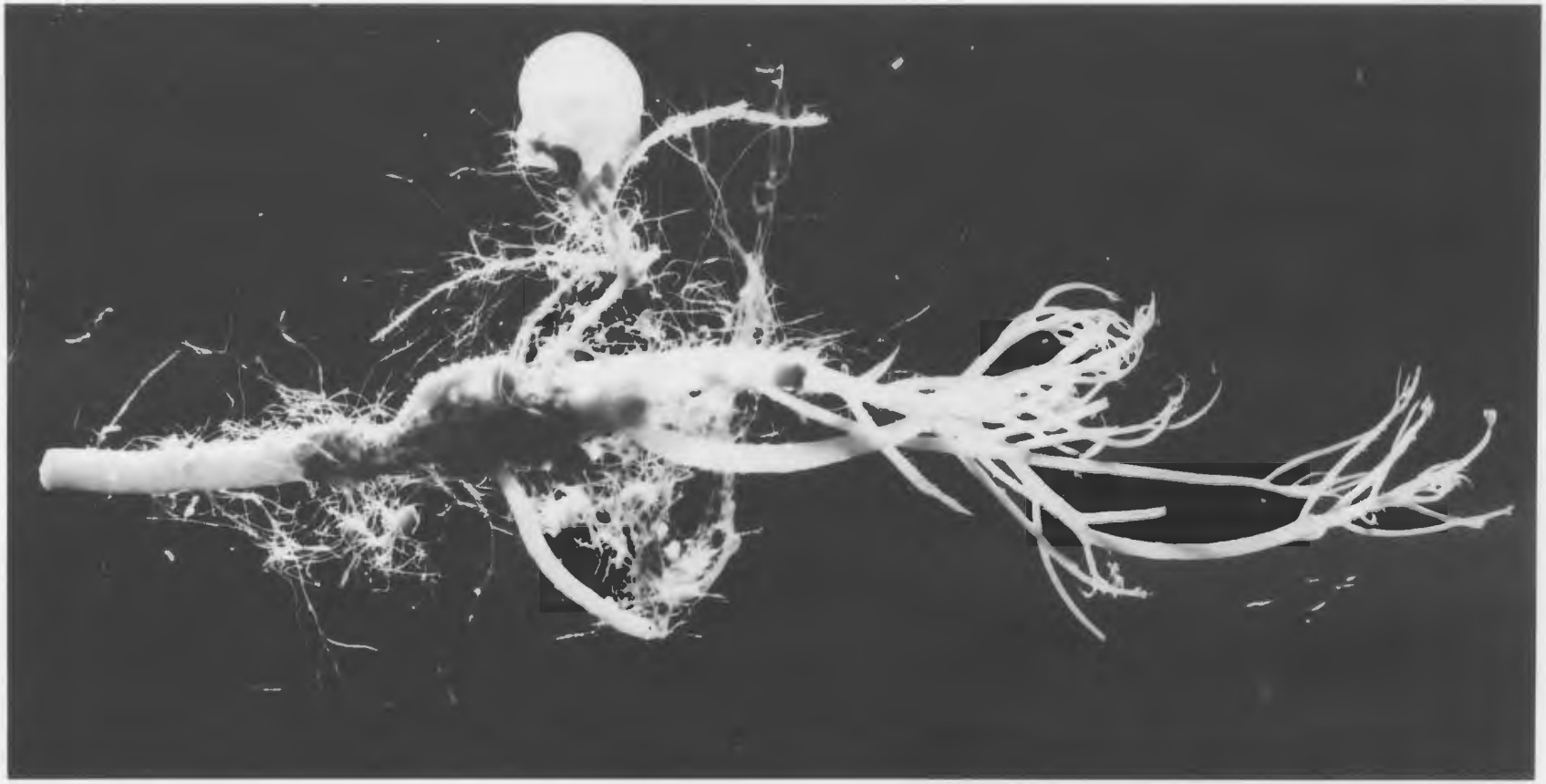


Fig. 35. Recently-settled scallop attached to the red alga, *Rhodermela conferroides*. (Alga identified by Dr. G. R. South.)

Size distribution of the first growth ring

The size distributions of the first growth ring of scallops from Port au Port Bay are shown in Fig. 36. At least two widely spaced peaks may be recognized in the scallops from Boswarlos bed; one at about 23 mm and a small peak at about 37 mm. The modes are less prominent in the scallops from West Bay and Fox Island River beds. It is suggested that the scallops with large first growth bands arise from early summer spawning and that those forming the larger mode but with smaller first growth bands arise from autumn spawning. All the distributions are skewed to the right.

It is also seen that there are minor peaks among the autumn-spawned scallops suggesting the existence of some kind of periodicity in the spawning process.

Symbiotic association with zoochlorella

Description of the alga

The following description of the organism is based on light microscope observations of plants *in situ* in the host and in culture.

Algal cells from the host are illustrated in Fig. 37A and B. Figure 37C shows plants from culture. While the species is unicellular, clumping is observed in culture. In the molluscan host the algal cells occur in large masses (Fig. 38, 39 and 46), but there is no evidence of a truly colonial habit. Cells from the host lack flagella, although there is a positive phototactic reaction in culture where colonies will spread entirely over the agar slopes (pers. comm. Dr. J. Stein, 1968).

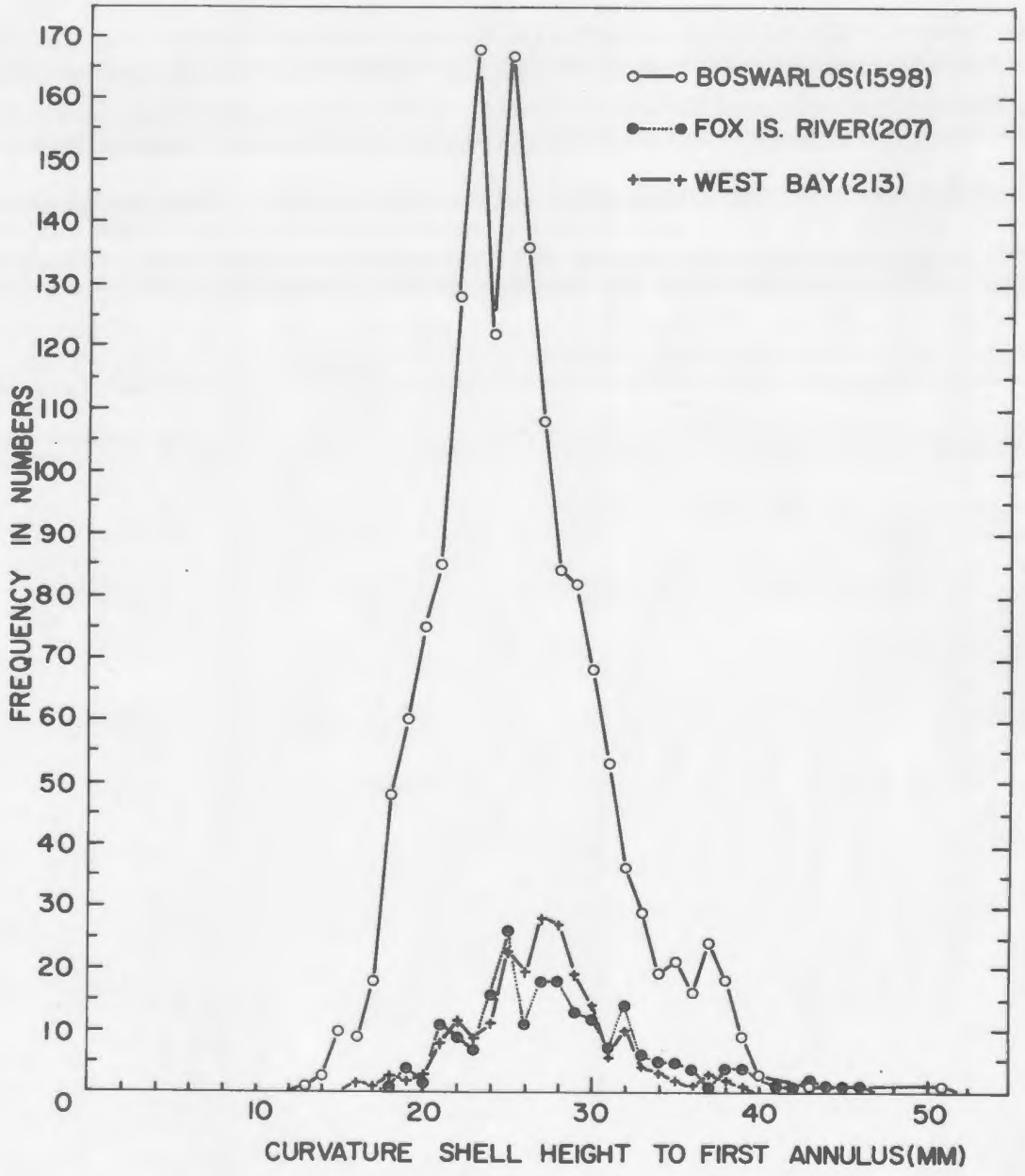


Fig. 36. Size distribution of the first growth ring.

The algal cells vary in shape and size and range from spherical to oval. Cells vary from 1.5 to 5.0μ (Fig. 37A, B and C). The cell wall is thick and usually colourless, although in old cultures individuals may occasionally be tinged yellowish-brown; there is no evidence from light

microscope observations of cell wall ornamentation. The 'anterior' end of the cell is commonly extended to form a blunt, hyaline tip (Fig. 37B); in some instances this tip has an apparent function in attachment of individuals during clumping, particularly in mature cells growing in agar and in liquid Erd-Schreiber culture.

Cells from both the host and from culture are bright green. One or two parietal band chloroplasts are present in young individuals, while in older ones the chloroplasts are frequently indistinct or subdivided (Fig. 37A). Storage products are as yet incompletely understood; in both natural and cultured populations cells do not give a positive starch reaction and no pyrenoids are obvious (pers. comm. Dr. J. Stein, 1968).

Reproduction is entirely by 4, 8 or 16 (most commonly 4) aplanospores, 1.5-2.0μ in diameter (Fig. 37B and C). Spores are released by rupture of the parent cell wall. Four aplanospores are typical of young cultures, while 8 or 16 typical of older cultures (pers. comm. Dr. J. Stein, 1968).

Dr. I. Friedmann (pers. comm. 1967) has provisionally identified the alga as a zoochlorella. Dr. Stein, however, on the basis of her study of cultured plants initially identified the alga as *Monodus amici-mei* Pascher (1914). (Class Xanthophyceae, Order Mischococcales, Family Pleurochloridaceae, in Park and Dixon 1968). She later withdrew this tentative identification on observing flagella in cultured plants.

The exact identity of the organism, therefore, remains uncertain. For purposes of discussion the broad term 'zoochlorella' is used throughout this paper.

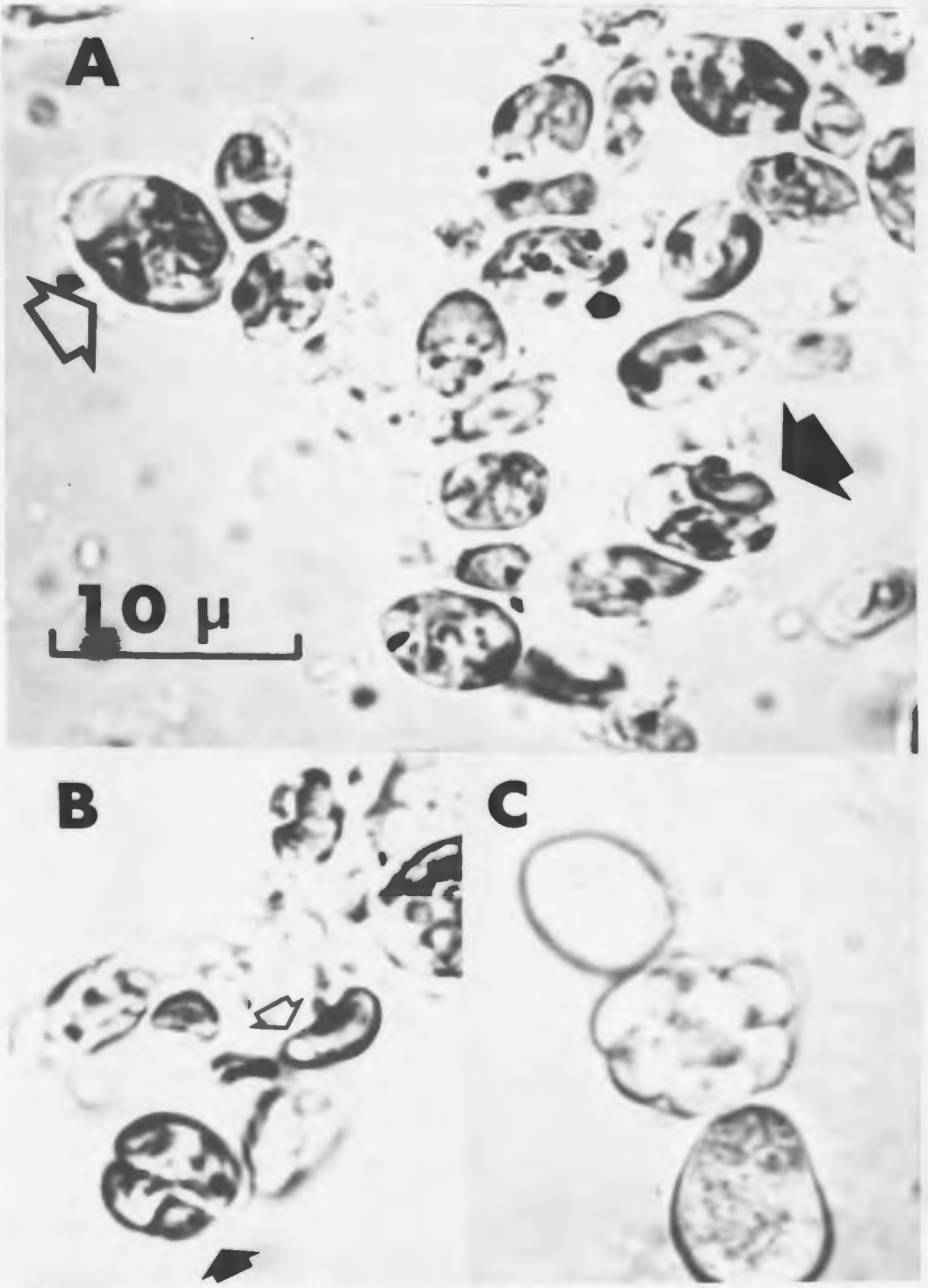


Fig. 37. A. Part of colony from scallop showing the characteristic arrangement of chloroplasts in young (solid arrow) and mature (open arrow) cells

B. Cells from host showing blunt hyaline tip (open arrow) and mature cell dividing into 4 aplanospores (solid arrow)

C. Mature cell from culture dividing into 8 aplanospores (solid arrow)

(Fig. 8A and B by Dr. R. South; Fig. 8C courtesy Dr. J. Stein).

Description of infection categories

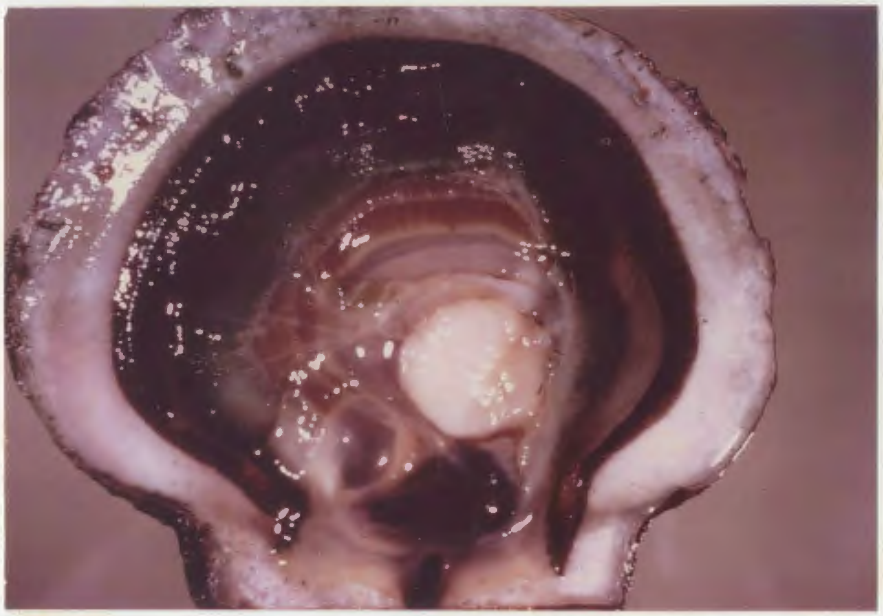
Uninfected (0): Algal colonies absent.

Light (L): Green algal colonies small; compact; confined to one or more localized points along mantle margin towards periphery of shell.

Moderate (M): Algal colonies spread over a greater area in the mantle and usually continuous throughout the mantle; infrequently small colonies of alga seen at the distal end of gonad.

Heavy (H): This is the extreme case and represents scallops which have been colonized for some time.

Heavily infected scallops characterized by luxuriant growth of alga spread over most of the potential areas of infection; both mantle tissues and distal end of the gonad covered with an immense number of colonies; bases of the posterior adductor muscle may also harbour some of the algal symbiont; colonies along mantle folds plentiful and dense giving mantle a uniform dark green colour (Fig. 38); alga frequently in patches on inside surface along ventral margin of shell; heavily infected scallops often laminated and unable to maintain tight closure of their shells and may have a musty odour.



Kodachrome II

Fig. 38. Giant scallop with right valve removed to show the intense green discolouration imparted to the mollusc by the presence of the unicellular alga (2/3 life size).

Areas of infection

As might be expected, the zoochlorella is especially numerous along those regions of the scallop within the shell most exposed to light. The preferred infection sites in the order of decreasing abundance are:

(i) Left (upper) and right (lower) mantle folds

(ii) Distal end of the gonad

(iii) Base of the posterior adductor muscle between the muscle and the left valve

(iv) Base of the posterior adductor muscle between the muscle and the right valve

(v) Sometimes what appears to be sloughed off colonies appear on the inner surface towards the shell edge of heavily infected scallops.

The principal areas of infection of the right mantle lobe of a moderately infected female scallop are shown in Fig. 39A. There is a decrease in the number and size of visible algal colonies from the mantle edge to the interior. Colonies lodged within the mantle are readily seen through the translucent tissues (Fig. 39B). This was later confirmed in histological sections of infected scallops (Fig. 40A and B). The mantle margin is the principal or preferred site of infection. The algal colonies are large and densely packed at the mantle edge but become sparse and scattered toward the interior of the host. The alga invades the gonadal and adductor muscle tissues secondarily after having colonized the preferred mantle region. Algal colonies on the gonad are superficial, diffuse and small (Fig. 41). A careful examination of the gonad is required to detect their presence there. Those on the bases of the adductor muscle are more dense, larger and appear in clusters. When infected it is the crescent-shaped posterior portion of the adductor muscle that usually contains the alga.

Areas of active ciliary activity such as the gills are conspicuously free of the alga. Table 24 shows the frequency of occurrence of the symbiont in the three potential areas of infection and the relative intensity of the infection within the tissues containing it.

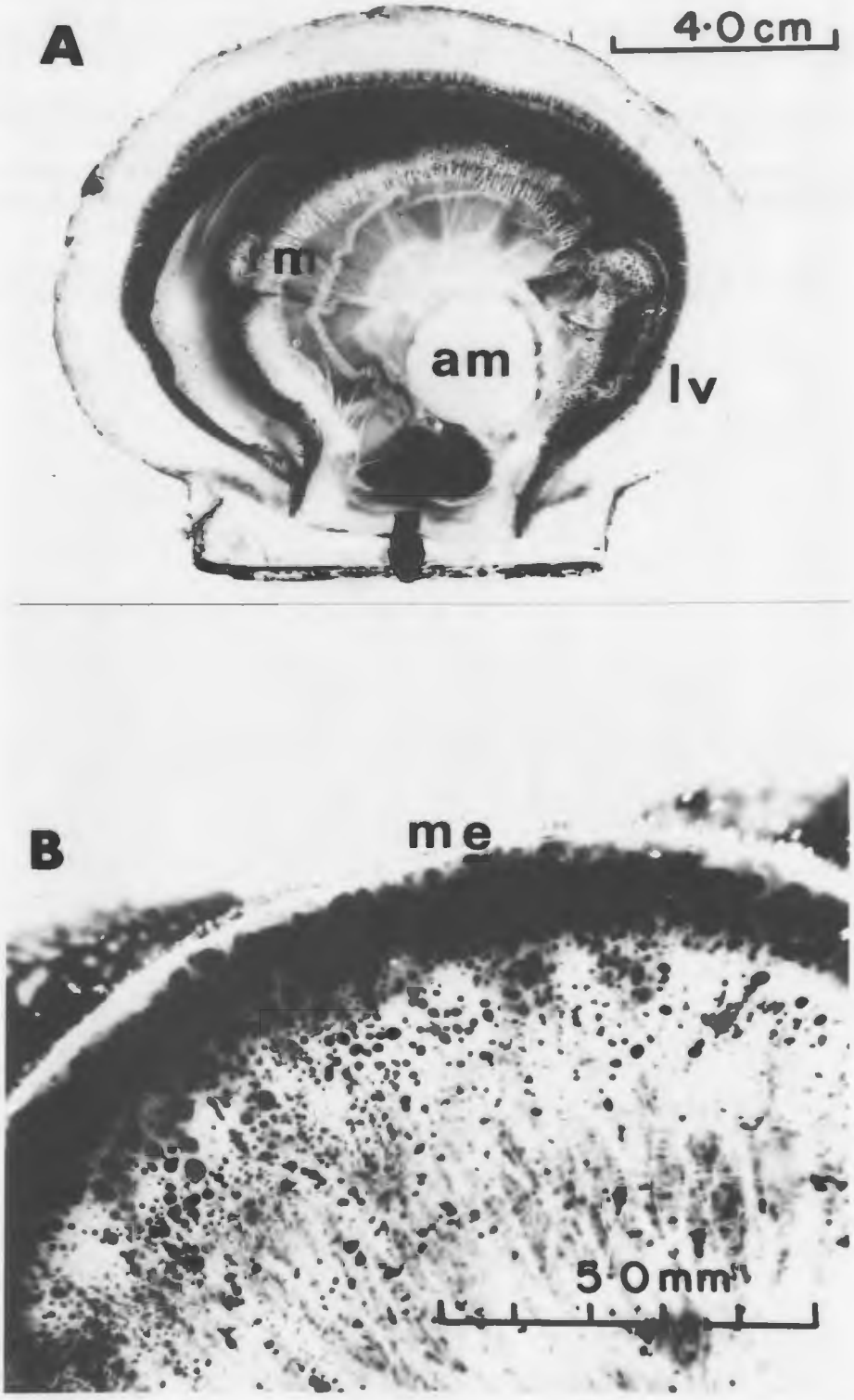


Fig. 39. A. A moderately infected 10-year-old female scallop showing the extent of algal infection on the right mantle lobe; am. Posterior adductor muscle; rm. Right mantle lobe; lv. Left valve

B. Enlarged surface view of mantle margin showing the decrease in the number and size of algal colonies from the edge of the mantle to the interior; me. Mantle edge.

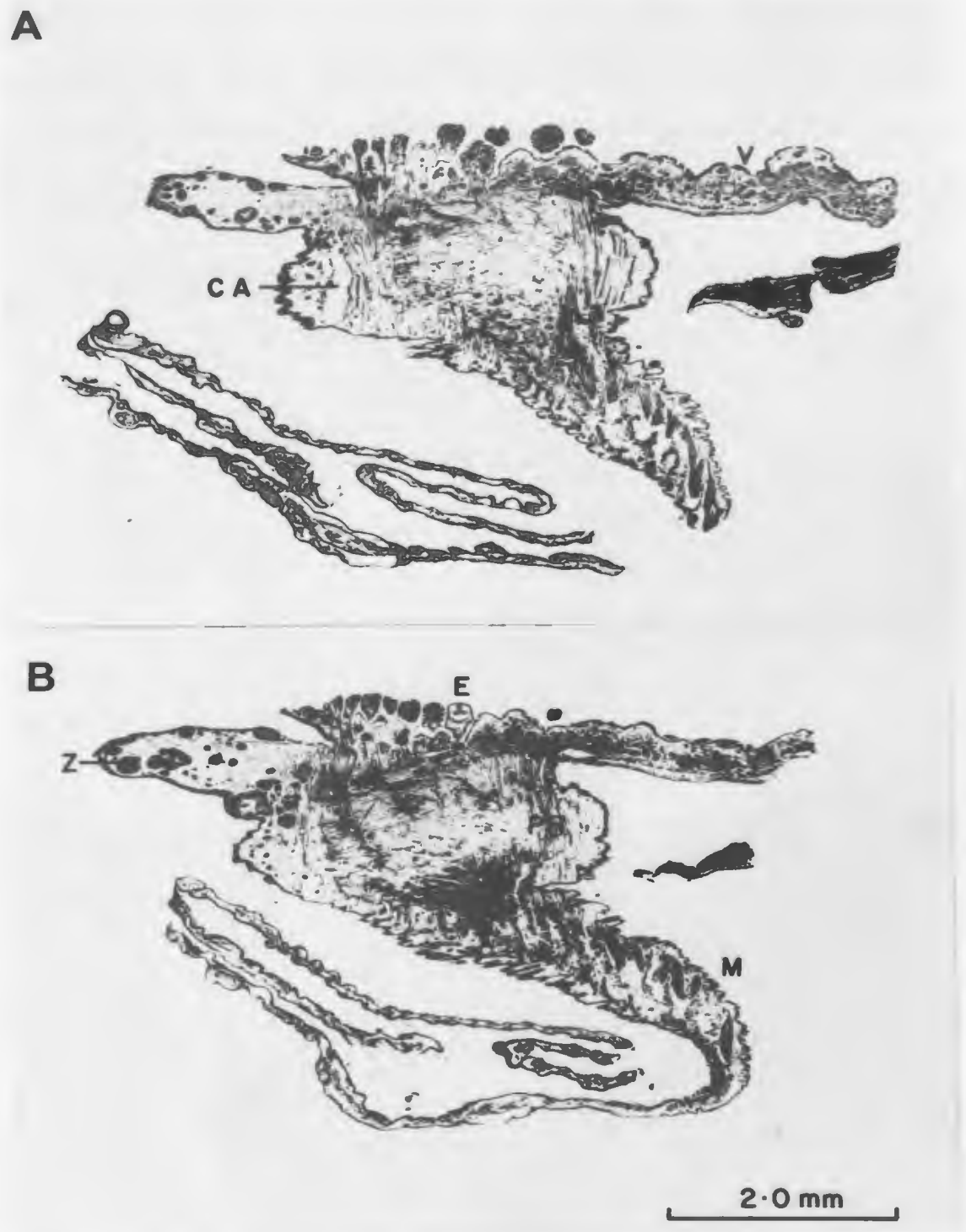


Fig. 40. Gross histological sections of the left (A) and right (B) mantle lobes of an infected scallop showing the distribution of algal colonies within the tissue. Colonies are particularly abundant in the outer mantle lobes and the left or upper mantle fold of the scallop; E. Eye; V. Velum; M. Mantle fold; CA. Circumpallial artery; Z. Zoochlorella; PR. Pallial retractor muscles.

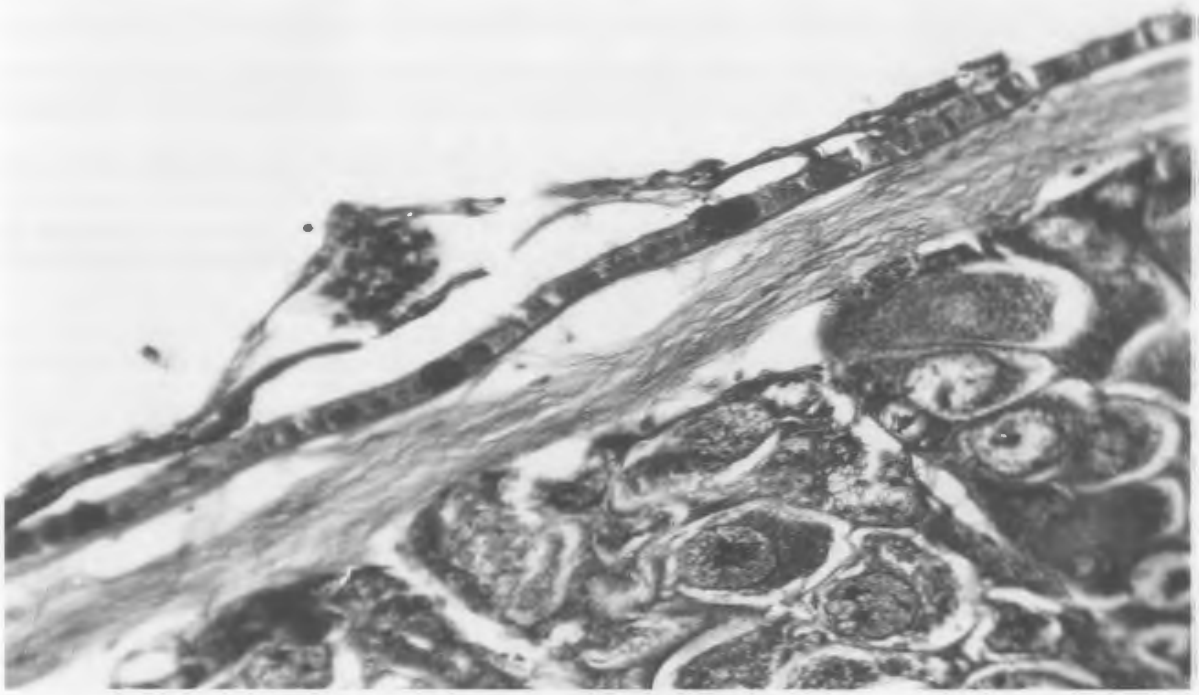


Fig. 41. C.S. of the gonad at 7μ showing a single superficial algal colony on the gonad epithelium.

Table 24. Preferred infection sites and the intensity of algal infection of the giant scallop, *P. magellanicus*, for a total of 2962 scallops examined from the Boswarlos bed, Port au Port Bay, Newfoundland.

Infection site	No. of infected scallops	Relative degree of infection			
		0	L	M	H
Mantle	521	2441	171	179	171
Gonad	88	2874	75	12	1
Adductor muscle base	79	2883	58	12	9

Incidence of the algal symbiont

The frequency of occurrence of the algal symbiont with depth from the four areas is given in Table 25.

Table 25. Incidence of the algal symbiont in *P. magellanicus* from four widely separated areas.

Area	Depth range (fm)	No. of scallops examined	Frequency of infection (%)	
			All ages	8 yrs and over
Port au Port Bay, Nfld.				
(a) Boswarlos bed	4-8	2962	17.6	42.5
(b) West Bay bed	6-7	215	3.7	3.3
(c) Fox Is. River bed	16-20	98	0.0	0.0
St. Mary's Bay, Nfld.	7-10	150	37.3	37.3
Bonavista Bay, Nfld.	6-15	81	21.0	21.0
Georges Bank	45-47	30	0.0	0.0

Scallops from St. Mary's Bay, Newfoundland gave the highest overall incidence of the alga. These overall percentages, however, are not directly comparable because of a bias in the samples collected by SCUBA diving. Only large scallops, 8 yrs and over were represented in the samples from St. Mary's and Bonavista Bays. By comparing the percentage infection rates for scallops 8 yrs and over from all sampling areas (Table 25,

last column) it can be seen that there is an inverse relationship between percentage infection and depth. There were no infections in the deeper water scallops examined from the Fox Island River bed and the Georges Bank area.

There does not appear to be any difference in the frequency of infection with respect to the sexes. Among 2435 uninfected scallops from the Boswarlos bed, 50.6% were males, 48.1% were females and 1.3% were hermaphrodites. Among the 520 harbouring the algal symbiont 47.3% were males, 51.7% were females and 1.0% were hermaphroditic.

The relation between frequency and degree of infection within each age group of scallops is shown in Table 26. The alga is not present at all stages of development, but occurs primarily in the older specimens. There is at first a pronounced increase in the incidence of the algal symbiont with age. The overall maximum of 56.4% occurs in 8-year-old scallops. The frequency of infection then gradually falls off as the higher age groups are reached.

There is a positive relationship between impaired shell growth resulting in the stunting of one or both valves of the scallop and the presence of the algal symbiont. Various types of shell growth impairment were observed in the present study (Fig. 42 and 43). The alga is frequently present and restricted to areas immediately surrounding regions of epifaunal associations (Fig. 42A and B) or in areas overgrown by *Lithothamnia*. Sometimes the shell edges become laminated into separate and distinct layers with two or more lips or laminae (Fig. 43 A-D). The alga is almost always predictably present in old, laminated thick-shelled specimens (Table 27).

Table 26. Relative degree of algal infection with age of the giant scallop for the Boswarlos bed in Port au Port Bay, Newfoundland (sexes combined).

Age in yrs	No. examined	Relative degree of infection				No. infected	% infection
		0	L	M	H		
0	1	1	0	0	0	0	0.0
1	43	43	0	0	0	0	0.0
2	192	192	0	0	0	0	0.0
3	454	454	0	0	0	0	0.0
4	226	222	3	1	0	4	1.8
5	399	392	7	0	0	7	1.8
6	366	354	7	3	2	12	3.3
7	157	137	6	3	11	20	12.7
8	133	58	21	21	33	75	56.4
9	274	152	31	49	42	122	44.5
10	334	181	53	49	51	153	45.8
11	249	156	31	37	25	93	37.3
12	94	66	10	11	7	28	29.0
13	28	24	1	3	0	4	14.3
14	9	6	1	2	0	3	33.0
15	3	3	0	0	0	0	0.0
	2962	2441	171	179	171	521	17.6

0 = no infection, L = light infection, M = moderate infection and H = heavy infection.

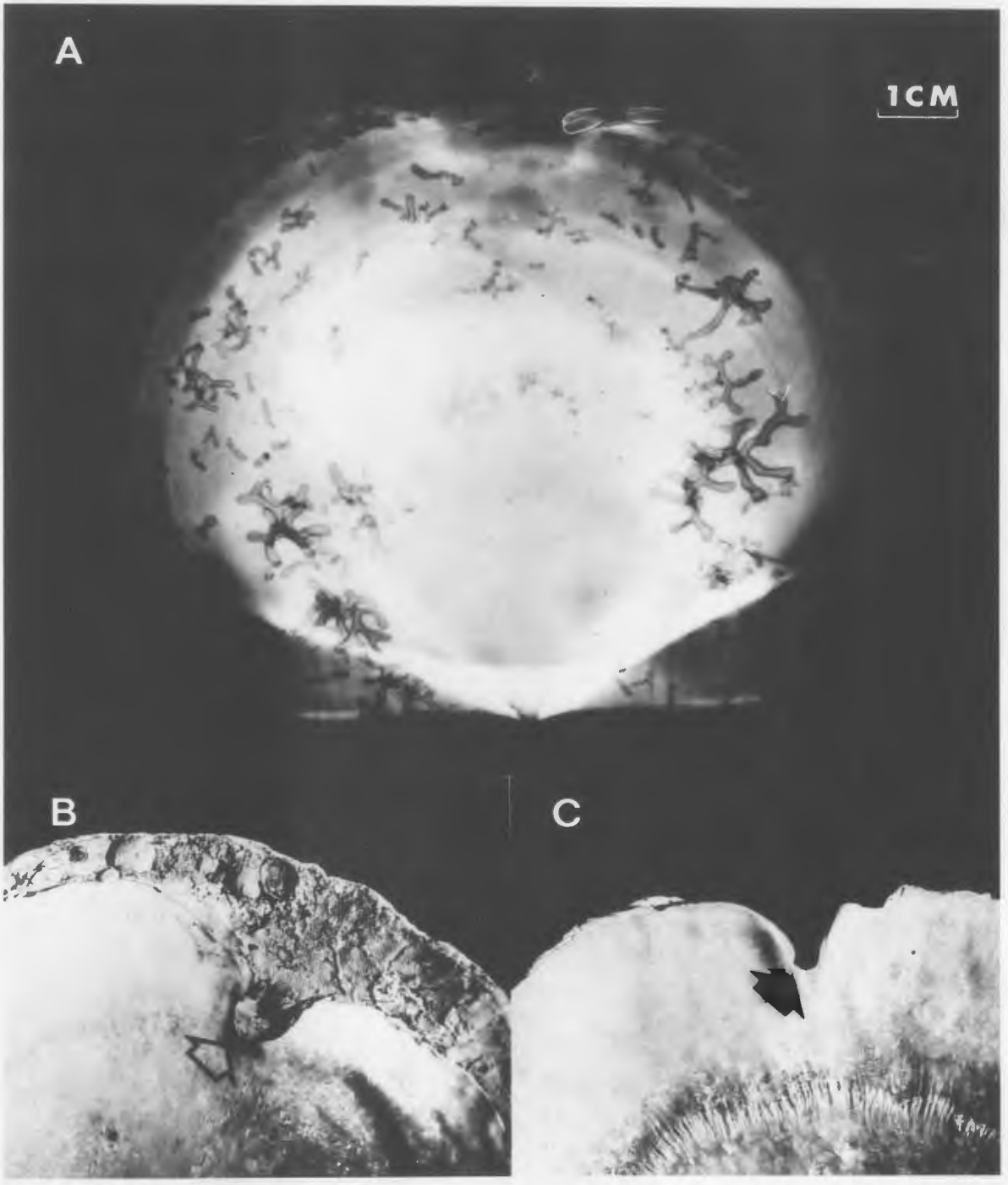


Fig. 42. A. Radiograph of a live infected scallop showing mussels attached to the periphery of the shell. The shell of this 10-year-old scallop has been undermined by boring animals including *Polydora* sp.

B. Recession of the inner nacreous layer in the left valve.

C. Complete recession of shell edge in the left valve.

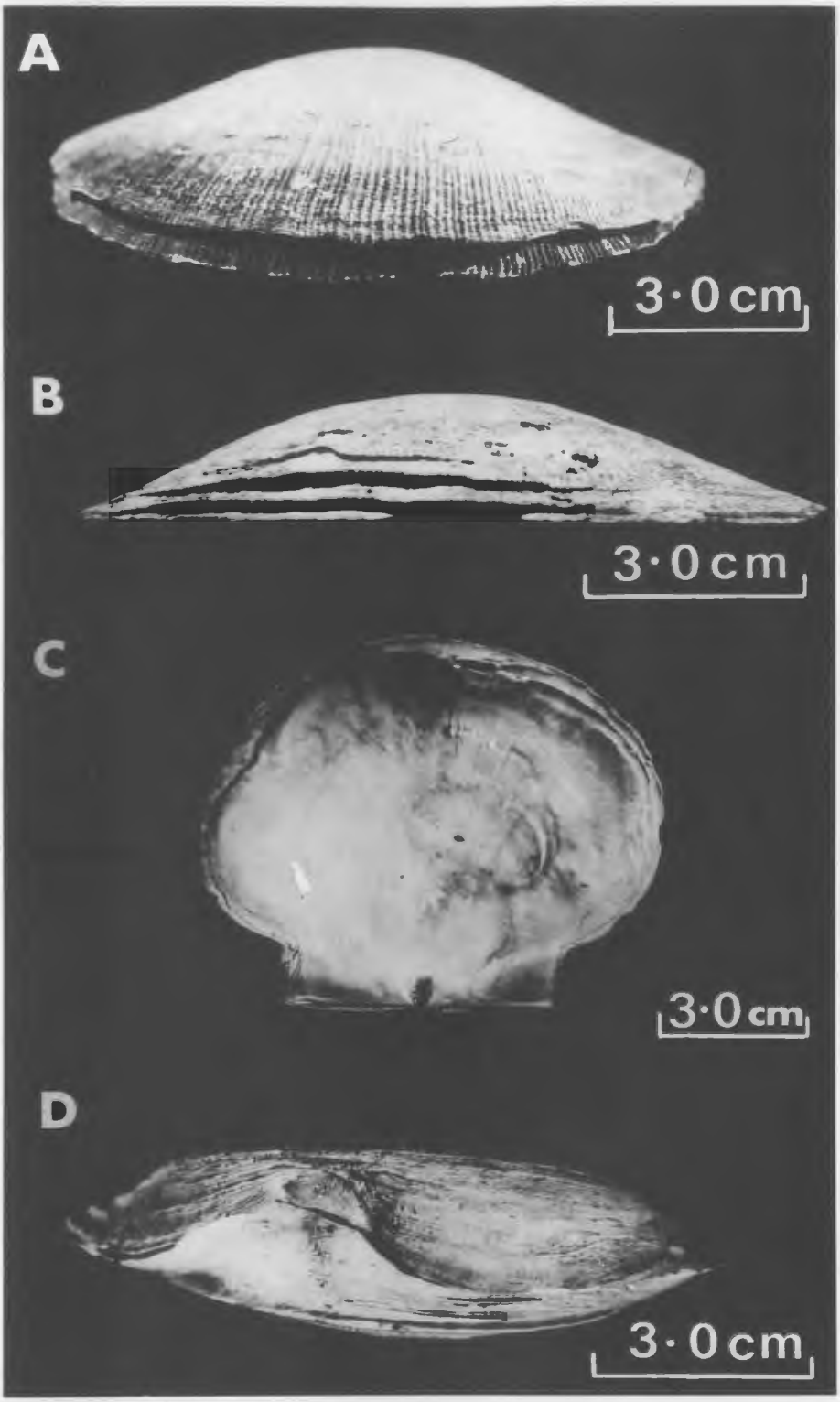


Fig. 43. Some types of shell abnormalities associated with the occurrence of the algal symbiont; A. Laminated left valve with two lips; B. Heavily laminated left valve with several lips; C. Same shell as in (B) showing inner surface; D. Ventral view of a highly deformed scallop.

Table 27. Incidence of zoochlorella in *P. magellanicus* with (A) normal and (B) laminated shells.

Shell condition	Year	No. examined	No. infected	No. uninfected	% infection
Normal (nonlaminated)	1966	1853	257	1596	13.9
	1967	926	85	841	9.2
	Total	2779	342	2437	12.3
Laminated	1966	161	157	4	97.5
	1967	22	22	0	100.0
	Total	183	179	4	97.8

Of the 183 scallops with laminated shell edge 179 contained the alga giving an overall infection of 97.8%. Only 12.3% of the nonlaminated shells gave infections of which the majority were light and were attributable to infections arising through factors associated with localized shell damage.

The alga is also found in mantle tissues surrounding areas of shell recession. This usually involves the nacreous layer which fails to reach the shell edge. Sometimes, however, all the three layers of the shell may be recessed giving rise to an indentation in the outline of the shell (Fig. 42B and C).

One of the scallops, uninfected at the time of tagging, was recaptured 56 weeks after release and contained the algal symbiont at two points along the mantle edge. From the position of the shock marks on the

shell it was clear that the infection had set in immediately after tagging. There was localized damage at two points along the shell margin and it was precisely at these points that the scallop carried the alga.

Monthly infection rates from May to November for the two years for which observations were made are given in Table 28.

Table 28. Monthly infection rates for the giant scallop from the Boswarlos bed for 1966 and 1967.

	1966			1967			Percent
Month	No. of scallops examined	No. of scallops infected	Percent infection	No. of scallops examined	No. of scallops infected	Percent infection	infection years combined
May	219	100	45.7	208	21	10.1	28.3
June	329	102	31.0	332	43	13.0	21.9
July	346	51	14.7	116	20	17.2	15.4
August	518	78	15.1	109	8	7.3	13.7
September	367	61	16.6	17	0	0.0	15.9
October	116	13	11.2	166	15	9.0	9.9
November	119	9	7.6	-	-	-	7.6
Totals	2014	414	20.6	948	107	11.3	

Individual samples examined from May to November gave infections varying from 45.7% in May to 7.6% in November for 1966. The monthly percentages for 1967, although generally lower than for the corresponding periods of the

previous year fail to show a pattern suggestive of a seasonality in the occurrence of the infection. Taking the two years together there is a gradual decrease in the incidence of the algal infection from May to November. Infected scallops do not lose or eject the alga during winter.

Effect of the alga upon the scallop

A range of variations was encountered in the effect of the alga upon the molluscan host. Light but visible infection does not apparently cause any easily discernible damage to the host. With heavier infection the scallop progressively develops more severe symptoms and a gradual decrease in the condition of the visceral mass including the adductor muscle is observed. The water retaining capacity of the scallop decreases and there is a gradual loss in the total body weight. In the extreme case the muscle becomes atrophied and stringy in consistency and suffers a gradual loss in weight. Heavily infected 8-year-old scallops, for example, have an average muscle weight of 27.4 g; uninfected scallops of comparable age have an average muscle weight of 35.1 g. The loss in muscle weight is accompanied by a decrease in the adductor muscle scar area. Affected tissues, especially the mantle, become slippery due to the presence of a large amount of slime which has a musty odour. Heavily infected scallops are unable to maintain a tight closure of their shells.

The following linear least square regressions have been calculated for different variates on age for both infected and uninfected scallops. In these regressions only those ages in which both groups were represented were used. All infected scallops are pooled regardless of the intensity of infection. Although the relation of the four variates examined

is not strictly linear with age, it is seen that for the ages used in the analyses, linearity may be assumed (Fig. 44 and 45) (A. Uninfected scallops; B. Infected scallops; t. Age).

I. Adductor muscle weight, Wm

A. $Wm = 3.12t + 3.55$ . . . . . (28)

B. $Wm = 2.30t + 3.88$ . . . . . (29)

II. Left adductor scar area, Sa

A. $Sa = 0.146t + 0.57$ . . . . . (30)

B. $Sa = 0.120t + 0.65$ . . . . . (31)

III. Body weight (excluding adductor muscle), Wb

A. $Wb = 9.90t - 0.22$ . . . . . (32)

B. $Wb = 9.27t + 1.77$ . . . . . (33)

IV. Wet shell weight, Ws

A. $Ws = 23.80t - 3.77$ . . . . . (34)

B. $Ws = 21.75 + 12.10$ . . . . . (35)

An analysis of covariance indicates that the difference in linear regressions of adductor muscle weights on age between infected and uninfected scallops is highly significant (Table 29). The regression lines, together with mean sample value at age, are shown in Fig. 44A.

Table 29. Analysis of covariance of regression of adductor muscle weight on age of infected and uninfected scallops.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	2268	74753.11	32.96
REG. COEFF.	1	767.02	767.02
COMMON	2269	75520.13	33.28
ADJ. MEANS	1	18075.42	18075.42

Comparison of slopes F = 23.27

Probability of random occurrence 0.000**

Adductor muscle scar areas of infected and uninfected scallops are plotted against age in Fig. 44B. The rates of adductor scar area increase in the two groups are significantly different at the 5% level but not at the 1% level (Table 30). The significant difference in the scar areas between infected and uninfected scallops would also support the hypothesis of a prolonged association between the alga and the scallop. The scar area is not as sensitive an indicator of muscle dimension/condition as is the adductor muscle weight and only a prolonged association can account for the difference in the scar areas between infected and uninfected scallops.

Figure 45A gives the age body-weight relationship of infected and uninfected scallops. There is no significant difference in slopes (P = 0.615) but regressions differ significantly in elevation (Table 31).

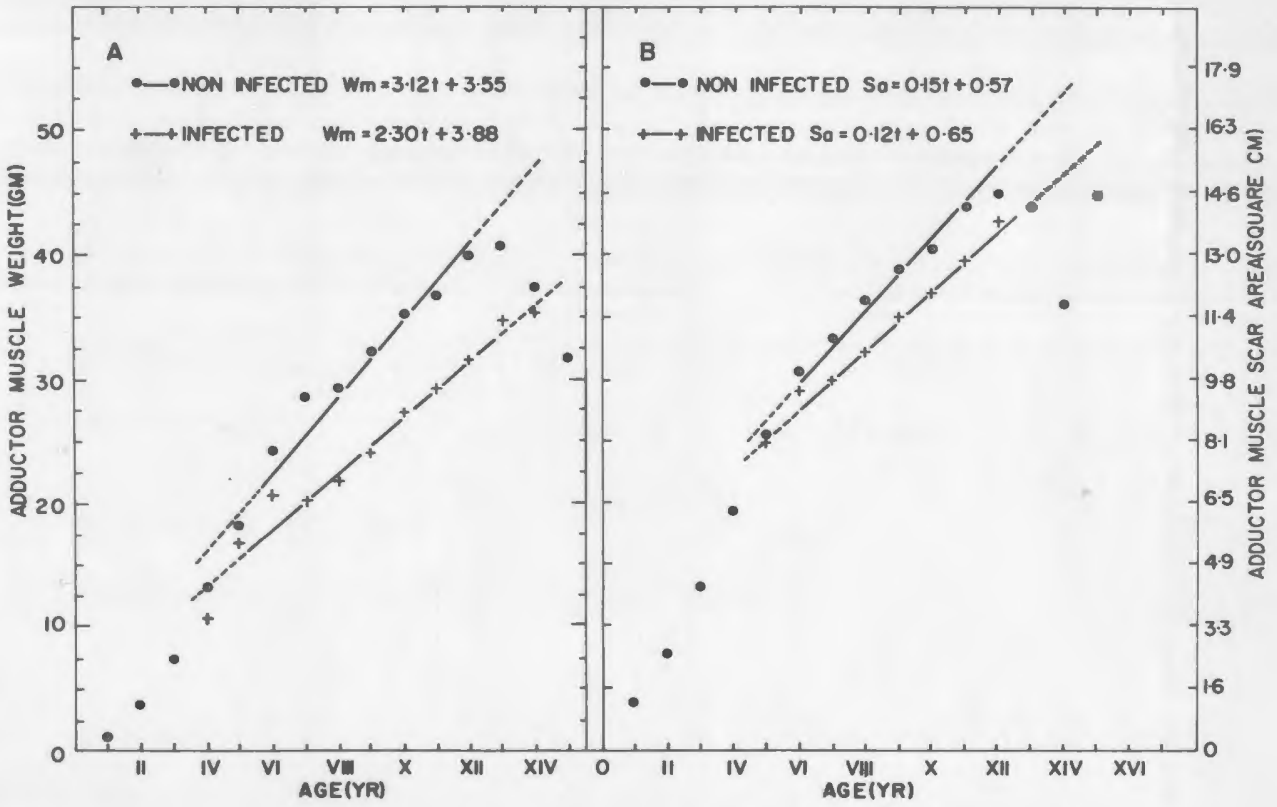


Fig. 44. A. Weighted linear regressions of adductor muscle weights on age for infected and uninfected scallops. Mean muscle weights at each age for the two groups are shown.

B. Weighted linear regressions of adductor muscle scar areas on age for infected and uninfected scallops. Mean scar areas at each age for the two groups are shown.

Table 30. Analysis of covariance of regression of left adductor scar area on age of infected and uninfected scallops.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	799	49.75	0.0623
REG. COEFF.	1	0.265	.265
COMMON	800	50.01	.0625
ADJ. MEANS	1	4.23	4.23

Comparison of slopes F = 4.25

Probability of random occurrence 0.037*

Table 31. Analysis of covariance of regression of body weight on age of infected and uninfected scallops.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	933	257562.85	276.06
REG. COEFF.	1	212.02	212.02
COMMON	934	257774.87	275.99
ADJ. MEANS	1	3399.60	3399.60

Comparison of slopes F = 0.77

Probability of random occurrence 0.615

Comparison of adjusted means F = 12.32

Probability of random occurrence 0.001*

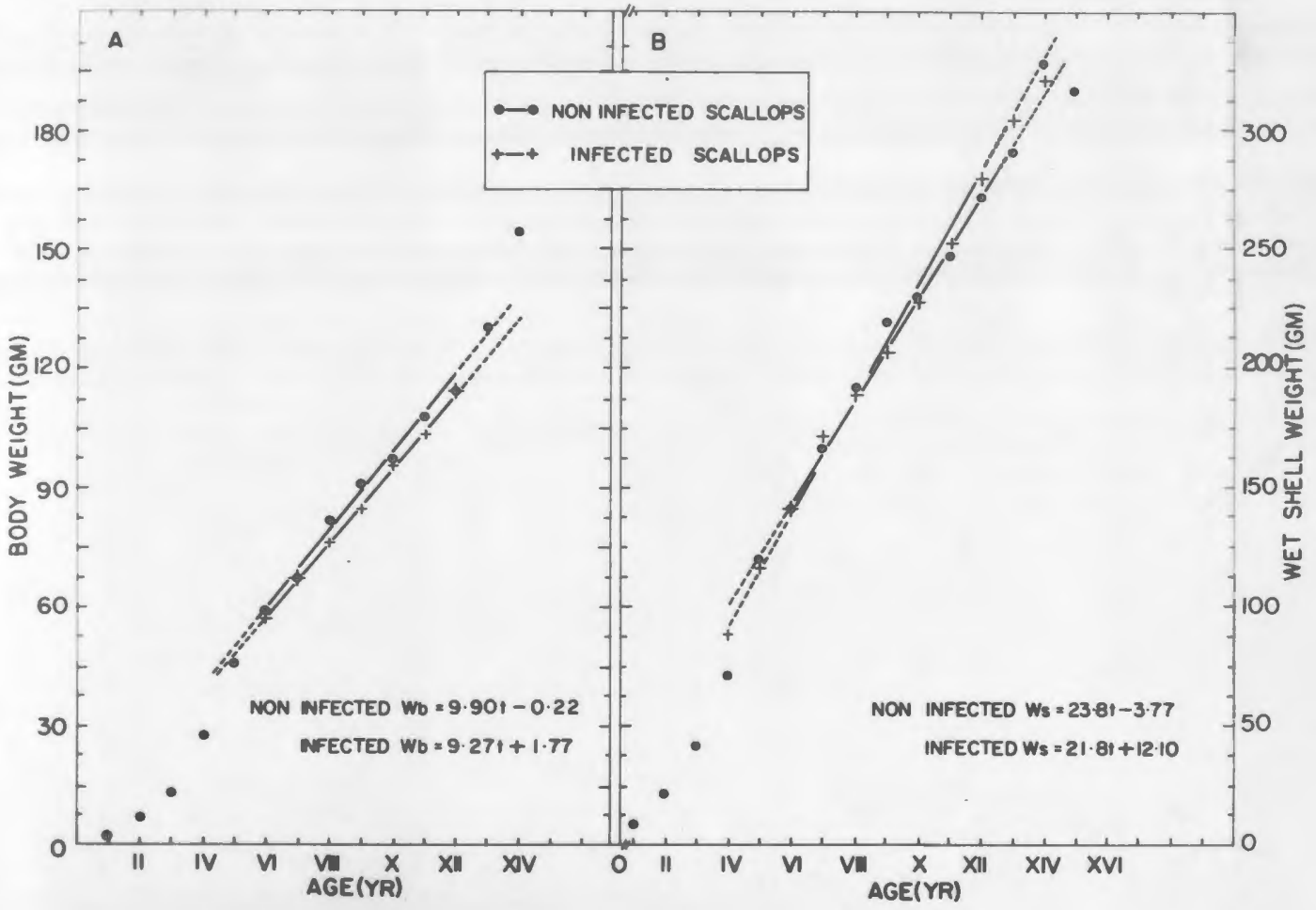


Fig. 45. A. Weighted linear regressions of body weight (excluding adductor muscle) on age for infected and uninfected scallops. Mean body weights at each age for the two groups are shown.

B. Weighted linear regressions of wet shell weight on age for infected and uninfected scallops. Mean shell weights at each age for the two groups are shown.

Finally an analysis of covariance showed that there was no significant difference either between the slopes ($P = 0.087$) or adjusted means ($P = 0.193$) of wet shell weights against age for infected and uninfected scallops (Table 32, Fig. 45B).

Table 32. Analysis of covariance of regression of wet shell weights on age of infected and uninfected scallops.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE
WITHIN	1484	1760052.6	1186.02
REG. COEFF.	1	3399.90	3399.90
COMMON	1485	1763452.5	1187.51
ADJ. MEANS	1	1982.40	1982.40

Comparison of slopes F = 2.87

Probability of random occurrence 0.087

Comparison of adjusted means F = 1.67

Probability of random occurrence 0.193

The consistent differences between infected and uninfected scallops in the regressions of the soft parts of the mollusc against age suggest that the algal infection has an adverse effect on the scallop. The alga, however, is not highly pathogenic and does not cause a rapid death of the host. This was shown by the return of tagged infected scallops that were at large for some 12 weeks. Heavily infected scallops are more prone to die than uninfected ones when kept in sea water that is not continually aerated. The presence of the alga on the tissues does not cause the deposition of nacreous material by the molluscan host; nor does it cause the deposition of a less than normal amount of shell material.

There is no evidence to suggest that the algal association impairs or precludes normal gametogenesis in the scallops.

Histopathological changes in mantle tissue

Histological and histochemical examination of infected mantle tissue revealed that the alga elicits encapsulation. Colonies are usually spherical and vary considerably in size ranging from about 10μ to over 300μ in diameter (Fig. 46). Some of the algal colonies, especially the larger ones, are surrounded by a network of collagenous fibres (Fig. 46C and D). The ground substance gave positive acid mucopolysaccharide staining with Alcian blue (Steedman, 1950) and is probably due to the presence of mucotin sulphuric acid in the connective tissue mucins. In spite of the fibrous encapsulation of host origin, the alga appears to develop normally within the tissues of the host.

Responses of infected gonad epithelial tissue and the muscle tissue were not investigated.

DISCUSSION

Age and growth studies

Age in molluscs may be determined by size-frequency studies, tagging-recovery experiments and interpretation of shell annuli (Haskin, 1954). Size-frequency studies on most bivalves, including the giant scallop, are of little value as spawning is protracted and recruitment irregular; the size ranges of older year-classes greatly overlap. The annual ring

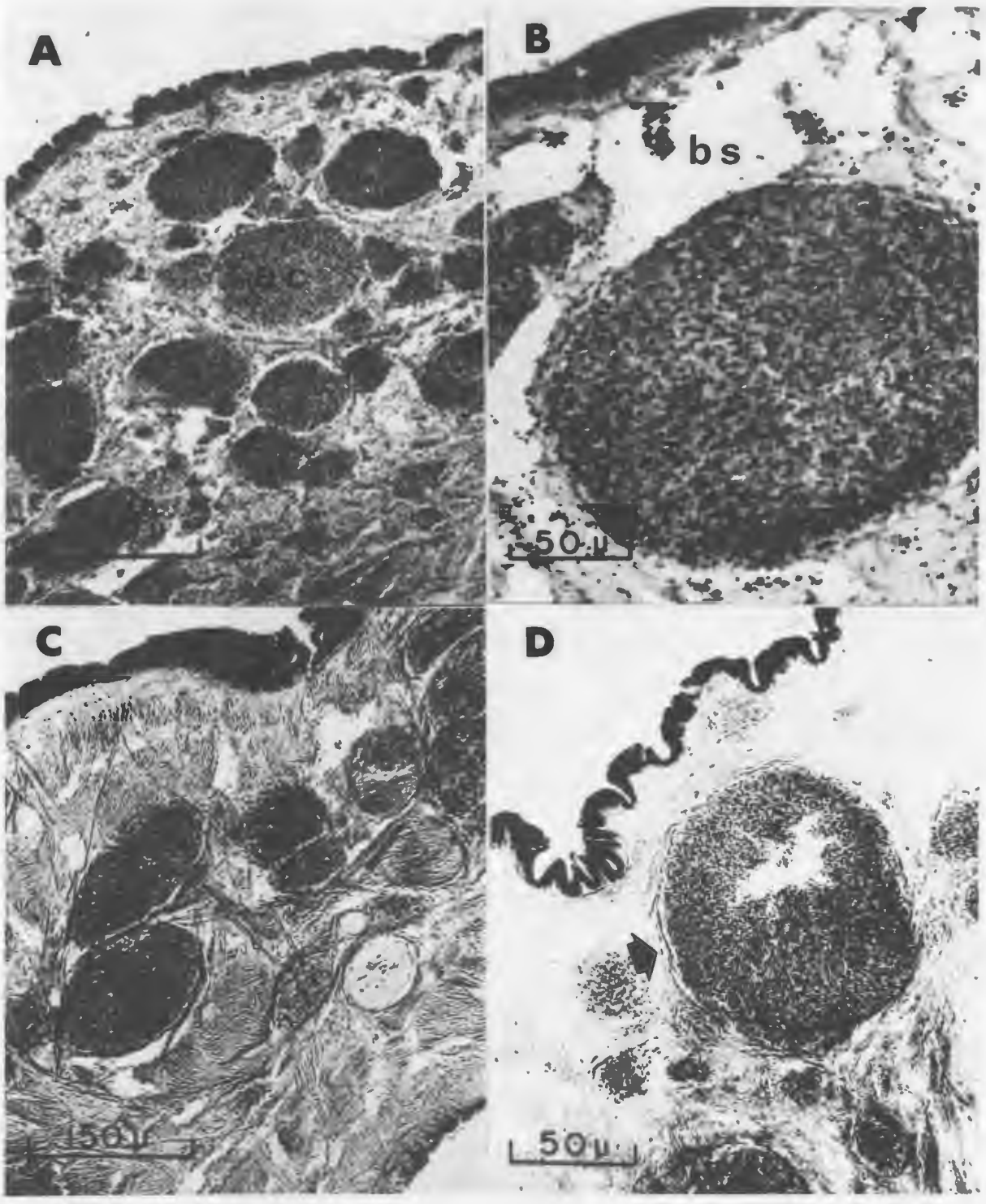


Fig. 46. A and B. Photomicrographs of frozen mantle section of an infected scallop at 10µ showing (A) numerous algal colonies (ac) lodged within the tissues (B) a single colony and its proximity to blood sinuses (bs) within the mantle.

C and D. C.S. of mantle tissue at 7µ showing (C) Numerous encysted colonies of the alga (stained with Masson's trichrome) D. Fibrous encapsulating strands of host origin (stained with Alcian blue - Chlorantine red). Photo by Dr. R. South.

method is the most direct and perhaps the best of the three methods and has been used successfully in the present investigation. The annual nature of growth rings in scallops in general has been demonstrated by several workers. Stevenson and Dickie (1954), Dickie (1955), Posgay (1953), Merrill *et al.* (1966) working on the giant scallop, *P. magellanicus*, Mason (1957) investigating into *Pecten maximus* have, for example, shown agreement between the number of rings on the surface of the shell and the age of the scallop. Cassie (1955) working on the lamellibranch Toheroa, *Amphidesma ventricosum* Gray, pointed out the occurrence of alternate light and dark regions in structures other than the shell and showed that the rings on the resilifer depression and on the broken ends of the resilia were in fact annual. Merrill *et al.* have also found this to be true in the giant scallop and have successfully aged the mollusc using the calcareous portion of the resilium or the impressions on the resilifer depression.

The giant scallop in Port au Port Bay is close to the northern limit of its distribution range and exhibits features of growth which appear to reflect wide annual fluctuations in temperature characteristic of the shallow-water environment. Annual rings are particularly well recorded on the shell surface. With the exception of *Lithothamnia* sp. which is often found in the umbonal region of Port au Port Bay scallops, epifaunal organisms on the shell surface such as *Anomia* sp. and *Crepidula fornicata* were easily removed to expose the continuity of growth rings. Supernumerary rings found in Port au Port scallops may be ascribed to severe storms; shock rings caused by dredging activity of the fishing fleet

are not important in the present study. There is some evidence of a general constriction in the spacing of the concentric circuli in mid-summer and early fall. This is probably related to high summer temperatures and possibly to the onset of the major spawning in early fall. These closely spaced circuli do not, however, bear any resemblance to the prominent annual growth rings. Therefore, a considerable amount of certainty is attached to age determinations in the present study. Tagging was employed only to demonstrate that the growth rings were formed once a year thus validating the ageing method. The consistency of relative strength of year-classes from year to year would also support the validity of age determinations.

There has been some controversy regarding the position and time of formation of the first annulus in the giant scallop (Merrill *et al.*, 1966). It has been shown here that the first visible ring on the left valve is formed during the second year of life. It is possible that juvenile scallops differ in their ability to record their first growth ring. Spring-spawned scallops in their first year may record faint annuli. Scallops arising from the late fall spawning do not appear to record a permanent growth ring. The shell of autumn-spawned scallops is probably too delicate and fragile at the end of the first winter to permanently record rings of any kind. The point, however, is that any ring formation occurring during or at the end of the first winter does not appear to be retained and does not show up in adults. Weak annuli formed by some scallops during the first year of life are either worn

away during active swimming of juveniles or frequently become obliterated by crustose corallines which almost without exception show their first appearance in the umbonal region of the left valve.

The time of formation of the growth ring in Port au Port Bay scallops varies from year to year and appears to take place about the time when active growth is resumed in early spring after an almost complete cessation of growth during the winter. Although the actual cause has not been demonstrated, Merrill *et al.* believe that it is the low winter temperatures.

Age composition

There are considerable variations in the year-class strength in scallops from Port au Port Bay. Similar variations in the success of year-class strength have been found or implied in the giant scallop from other areas (Dickie, 1955 and Merrill and Posgay, 1964) and in several other pectinid species: *Pecten yessoensis* Jay (Yamota, 1950); *Notovola meridionalis* (Tate), (Fairbridge, 1953 and Olsen, 1955) and *Pecten maximus* L. (Baird, 1966). The importance of year-class composition in the study of scallop populations has been well demonstrated by Dickie (1955). He showed that the abundance was high when recruited year-classes are strong, but low when they are weak. Dickie successfully correlated abundance of commercial-sized scallops in any one year to water temperatures six years previously. He concluded that changes in abundance of scallop stocks in the Digby area result from the combined action of temperature and circulation of pelagic larvae.

The age composition of Port au Port scallops before and during periods of heavy fishing is not known. The annual harvest in the early 1950's is, however, indicative of the existence of special conditions within the bay that serve to retain and concentrate scallop larvae that re-seed the beds in the bay. One of the main causes of year-class fluctuations within the bay may be inferred from the current patterns and larval transport in and out the Port au Port Bay system.

A current of water from the south of Newfoundland enters the Gulf of St. Lawrence at Cape Ray, Newfoundland. This current is deflected to the right, passes St. Georges Bay and touches the Newfoundland coast in the Bay of Islands area, from where it continues northward along the coast (Sandstrom, 1919). This current thus bypasses both St. Georges and Port au Port Bays. Since the influence of the current is not felt in these bays, the surface currents within them will be largely under the control of winds (Templeman, 1939). Templeman investigating into the life-history of the American lobster, *Homarus americanus*, on the west coast of Newfoundland successfully correlated the abundance of small lobsters in St. Georges Bay and their relative absence in Port au Port Bay to the prevailing south-westerly winds in July and August. On the west coast lobster eggs hatch out by July and complete their free swimming larval stage in just over a month. The prevailing south-westerly winds at this time of the year tend to hold the free swimming young larval lobsters along the north shore of St. Georges Bay and carry them out towards the Gulf of St. Lawrence in Port au Port Bay.

A similar phenomenon is indicated for the giant scallop in Port au Port Bay. The breeding cycle of the scallop in the bay is, however, slightly different for it spawns later in the year, usually during September-October, depending, among other factors, on water temperature. At this time north-easterly, north-westerly and westerly winds are more frequent and tend to retain larval stages in Port au Port Bay. These are eventually recruited into the beds within the bay. An analysis of weather records taken at Stephenville airport from 1955 to 1963 suggests that moderately calm weather and strong west and north to east winds during relatively warm years give strong year-classes, e.g. 1959, 1960 and 1962 year-classes. Whereas south-westerly winds during the breeding period of the scallop generally give poor year-classes, they are not as obvious or consistent in their effect as are the north-easterlies. It is suggested that south-westerly winds do not play as important a role in affecting larval transport as they do in St. Georges Bay. The impact of these winds is probably reduced by the cliffed shore highlands separating the two bays (p. 13). West-south-westerlies are perhaps more important in affecting larval loss from within the bay. The 1958 year-class in particular is very poorly represented. The generally poor weather conditions that year with WSW winds prevailing from July through October may be responsible for this. The relative absence of the 1958 year-class provides a measure of confidence in the age determinations.

In view of the relatively long larval period (about 40-50 days) wind-induced larval transport in surface waters from the fairly extensive scallop beds in the Bay of Islands area or even from St. Georges Bay into

Port au Port Bay is clearly possible and is not to be excluded. This may in part account for the build-up of particularly high concentrations of scallops within the bay. Templeman (pers. comm. 1969) suggests that as the larvae get larger and begin to form shell they keep well below the surface and hence are retained in Port au Port Bay by the deeper current of water which must flow into the bay when the surface water drifts out with the prevailing winds. Nutrients from land drainage probably also play an important role in the productivity of the almost enclosed Port au Port Bay system.

Relative proportions of year-classes from year to year on the Boswarlos bed during the 1966-68 period indicate that the stock has remained more or less stable and has simply aged by three years.

It is difficult to explain fully the relative absence of small scallops on the beds. To what extent this is a reflection upon the availability of juvenile scallops is not known. The taking of small scallops by gears specially designed to procure them, such as the one used in the present investigation, has often met with failure. Many investigators including Priol (1930), Tang (1941), Elmhirst (1945), Baird (1952), Fairbridge (1953) and Mason (1957) have noticed the scarcity of young scallops in the expected numbers. Baird and Gibson (1956) suggested the relative absence of small scallops as being due to either the existence of feeder beds from which juveniles migrate back to parent beds or possibly due to young scallops escaping the dredge. By direct observation on scallop beds they found no evidence to suggest migration from feeder beds and that there was little escape reaction. They concluded that tooth-spacing, the

only other selective feature of the dredge, must be the effective selecting agent. Mason (1957) took into account this selectivity and showed that the dredge still collected less than the expected proportion of young scallops. He concluded that in his study teeth were ineffective as a selecting agent as the dredge acted as a bottom-sampler. In the present investigation teeth-spacing may again be discounted in favour of an avoidance reaction by young scallops. Caddy (1968) has shown that swimming activity rather than drag selection is responsible for the low drag efficiency for the capture of scallops smaller than 100 mm and that small scallops can avoid approaching objects by swimming away from them. There is also a reliable report of a large number of young giant scallops seen at the surface in water as deep as 25 fathoms (cited by Posgay, 1963). The only explanation regarding the relative scarcity of small scallops may be associated with the active swimming behaviour of juveniles. Extensive migration of adults may be ruled out in view of the recovery of tagged scallops near the place of original release. Characteristic epifaunal associations and shell morphology would also suggest that there is no intermingling between the beds of the relatively sedentary adults.

Shell-height frequencies

The shell-height has been expressed as the distance from the umbo to the ventral shell margin measured along the curvature of the left valve. It is suggested that this is a more realistic estimate of shell growth than the straight tangential dorso-ventral measurement; for it measures the total column of shell secreted by the mantle irrespective of

shell-thickness. It thus corrects for shell curvature. In all previous studies of the giant scallop the dorso-ventral shell-height along a straight line tangential to the curvature of the left valve has been used. Marshall (1960) investigating into the biology of the bay scallop, *Aequipecten irradians*, however, used the distance along the shell curvature of the right valve. The only drawback in the method is that it is a little more time consuming than the direct method.

The modes in the shell-height frequency polygons for the 1966 Boswarlos collections (78, 118 and 148 mm) occur at sizes which correspond to the mean observed sizes of 3-, 5- and 10-year-old scallops respectively. Similarly the modes at 153 mm and 138 mm for the West Bay and Fox Island River beds both occur at mean shell-heights of 9-year-old scallops. The relative scarcity of 4-year-olds (1961 year-class) appears as a depression between 90-115 mm in 1966 and between 110-122 mm in 1967. The scarcity of the 1958 year-class (mean DA 135.5 mm) does not show as strikingly as in the height-frequency histograms. Only a slight depression occurs around 133 mm. This is undoubtedly due to the tremendous amount of overlap in shell-heights in the higher age groups.

The merging of modes in the greater shell-height groups also accounts for the progressive decrease in the spacing of the modes. The relatively slow progression of modal shell-heights in the older shells is suggestive of a declining growth rate and the attainment of a maximum shell-height characteristic of the bed. In addition to the declining growth rate, the relative stability of the right-hand side of the height-frequency distribution may also be due to the attainment of a final maximum size and the piling up of a number of year-classes within one large peak.

The more recent catches, together with the age and length composition data collected during the period 1966-68 suggest that the depleted stocks have recovered sufficiently from overfishing by exploitation during the early 1950's. Many local, small open-boat operators have been attracted to scallop fishing in the late summer months by both the relative abundance of commercial-sized scallops and the high financial return. Careful regulation will be necessary to ensure sustained yields, or alternatively the beds may be fished spasmodically.

Rate of growth

Beverton and Holt (1957) have shown that for some problems in population dynamics it is useful to describe the growth of fish in mathematical terms. While it is possible to approximate any growth data using the general polynomial function several workers have chosen to use the von Bertalanffy growth equation to describe growth in animals. One of the advantages of the von Bertalanffy equation is that its parameters, at least in theory, are in some way related to the metabolic activities of the animal. This is, however, yet to be convincingly demonstrated. The familiar von Bertalanffy growth curve has three parameters: L_∞, K and to. Attempts to relate L_∞ and K values to environmental factors have met with varying success, the results of one worker often contradicting that of another. Knight (1967) has pointed out the dangers of a mathematical tool and in particular of the von Bertalanffy growth equation and has emphasized that both K and L_∞ should be regarded as convenient descriptive summaries rather than laws of nature.

In the present paper von Bertalanffy growth curves have been fitted to selected shell dimensions of the giant scallop from Port au Port Bay. Growth rates have also been computed for other areas using published data. In considering the growth of the mollusc from different areas discussion is limited to the observed differences in growth patterns and only a brief mention is made of the possible correlation between the von Bertalanffy parameters and the environment.

The results show that within Port au Port Bay, West Bay scallops have a faster growth rate than the other beds examined. Scallops from the Fox Island River bed in particular have the lowest growth rate. The same conclusions are drawn in terms of between bed comparisons using three shell dimensions of the left valve. An examination of the von Bertalanffy parameters of shell-heights at age and their 95% confidence limits indicates complete overlap by L_∞ for the Boswarlos and West Bay scallops, and K for all areas. The L_∞ value for the Fox Island River bed does not, however, fall in the range of sizes observed for the Boswarlos and West Bay beds. K values appear to remain relatively constant for the three beds examined within the bay. This supports the argument of Beverton and Holt (1957) that K, which on theoretical grounds is independent of food consumption, will remain relatively constant, and that changes in growth rate may be reflected by variations in L_∞ or W_∞ (asymtotic weight). Beverton and Holt (1960) point out that within populations of a species living in different areas food and temperature account for most of the variation encountered. They argue that food supply modifies the asymtotic length while environmental temperature affects both K and L_∞ and that with increase in water temperature

K increases while L_∞ decreases. The reasoning of Beverton and Holt has been used to explain the findings in the present paper. We are here dealing with a confined shallow-water environment where hydrographic features (water properties) including temperature may be considered to have the same effect on all the beds. It is important to remember that the relatively sedentary scallop does not move around in search of food but rather feeds passively collecting what material is available immediately around it. The presence of genetically distinct populations within the bay can reasonably be discounted. Spawning on the three beds may be assumed to take place at approximately the same time during any one year. The pelagic larvae must be well distributed throughout the bay. Both morphological and growth-rate differences between scallops from different beds suggest the operation of factors peculiar to the beds themselves. It is suggested that the observed differences in L_∞ in the Boswarlos and West Bay beds as opposed to the Fox Island River bed must be associated more intimately with the immediate environment of the scallop.

The long standing concepts attributing favourable scallop conditions, at least in the bay scallop *Aequipecten irradians*, to water current effects (Belding, 1910; Gutsell, 1931; Marshall, 1960) have been questioned by Cooper and Marshall (1963). They have suggested that in view of the water volume available and filtered by scallops, current may not play as important a role as was previously thought. While the current patterns and the role of current influences have not been investigated it seems reasonable to assume that a similar state of affairs exists in the giant scallop.

The differential growth rate in the bay appears to be related more to the silt-clay content than to any other likely environmental factor operative in the bay. In the Port au Port Bay system, clayey silt and sand-silt-clay are the more important sediments although sand, gravel and small pebbles are important locally. The deeper parts of the bay contain a predominant silty organic mud-type of sediment (J. Shears, pers. comm. 1966). Lilly (MS, 1965) has made direct observations on the type of sediments forming the upper layers of the scallop beds in Port au Port Bay. He found muddy organic compacted silt with mixed pebbles up to 25 mm on the Boswarlos bed and loosely suspended organic silt and mud about 1 ft thick on the Fox Island River bed. Mixed silt, sand and gravel are the most common sediments on the West Bay bed. Dredging observations also suggest the occurrence of these sediments on the beds. Gravel and boulder train were frequently encountered on the Boswarlos bed. The depositional sites for the fine sediments may be the result of characteristic current patterns within the bay. The same current patterns would also tend to concentrate settlement of spat on the Fox Island River bed. This might explain why the Fox Island River bed is the largest and most prolific of beds within the system. The slower growth rate here may, however, be due to at least two factors peculiar to this bed.

Inhibition of scallop growth in fine sediments may result in part from the periodic interruption of feeding and the additional expenditure of energy required in keeping the filtering apparatus clean. Scallops lying recessed as they do in soft mud must inadvertently take in considerable amounts of fine silt. Loosanoff and Tommers (1948) have shown that suspended

silt has a pronounced effect on the pumping rate and hence the feeding of oysters; as little as 0.1 gm of silt per litre of water reduced the pumping rate 57%, and the oyster expelled large quantities of silt as pseudo-faeces. Both the soft-shell clam, *Mya arenaria* (Swan, 1952) and the quahog, *Venus mercenaria* (Pratt, 1953) have been shown to grow faster in sand than in mud. Pratt and Campbell (1956) investigating into the environmental factors affecting growth in *V. mercenaria* found that growth of the mollusc is retarded in sediments with a high silt-clay content. They related the observed inferior growth in fine sediments to the concomitant reduction in sediment permeability, accumulation of substances inimical to growth, and the more frequent expulsion of pseudo-faeces required of an efficient filter-feeder. Tenore *et al.* (1968) investigating into the effects of bottom substrate on the brackish water bivalve *Rangia cuneata* also found that clay-silt sediments were unfavourable as an environmental substrate. They suggested that physical and chemical factors associated with finer sediments were responsible for the adverse effect.

Although experimental evidence is lacking there is no reason to believe that scallops behave any differently. The suggested correlation between growth rate and silt-content becomes even more meaningful when the sources of nutrients of the scallop are considered. Davis and Marshall (1961) on the basis of an examination of stomach contents have suggested that in the bay scallop, *Aequipecten irradians*, the relatively smaller benthic and tychopelagic diatoms may be a more important source of nutrition to the scallop than planktonic forms. Casual observations suggest that much of the food in the giant scallop is also of benthic origin. Davis and

Marshall have indicated that scallops probably derive much of their food directly from the water at the level of the incurrent mantle opening, roughly ¼ inch off the bottom. This finding would emphasize and indeed lead us to expect a negative correlation between growth rate and silt-content.

The organic content of sediments may also be important. Bader (1954) states that, among other factors, the organic content of sediments and its state of decomposition apparently controls pelecypod densities. He found an increase in the densities of bivalves with a moderate increase of the organic matter concentration of the sediments. Tenore *et al.* have demonstrated the favourable effect of organic matter and phosphate on the growth of *Rangia* in sand sediments. High concentrations of organic matter and phosphate in clay-silt sediments, however, further increased the adverse effect on growth. They attributed this to the formation of a reduced oxygen-depleted environmental substrate.

A further observation supporting this negative correlation with silt-content is seen in the distribution of shell weights at age. A slower growth rate alone cannot account for the large differences in shell weights observed in the Fox Island River scallops. Some other local factor appears to be interfering with the ability of the animal to deposit shell material. While greater pressure in deeper waters may influence the rate of shell deposition, personal observations of shells from deep-water animals (20-30 fathoms) would suggest that the effect of pressure is not altogether important.

In addition to differences in growth rate caused by silt-content there is also the possibility of adverse crowding effects on the Fox Island

River bed. It has been shown here that scallop densities are higher on the Fox Island River bed than on the Boswarlos bed. The results of the density surveys must be interpreted with caution because only a very limited area was covered. Smaller scallops may have been easily missed because of poor visibility underwater or they could have avoided the grid by swimming away from it. It is well known that small scallops are more active and exhibit avoidance reactions (Caddy, 1968). Lilly (MS, 1965) reported concentrations up to 25 scallops per 20 ft square on the Fox Island River bed. Whatever the numerical abundance is, the important point here is to appreciate that densities are higher on the Fox Island River bed and that higher densities may result in crowding which in turn can cause adverse effects on the growth of the animal.

The results show that the West Bay and Boswarlos scallops have a faster growth rate than the Fox Island River scallops. The same conclusions are drawn for the three shell dimensions studied. But when one compares adductor muscle weights or adductor muscle scar areas of commercial-sized animals, West Bay scallops maintain the high yields as would be expected but the V^{+} and over Boswarlos scallops had the poorest condition in terms of muscle weights. This unexpected reduction in muscle weights and adductor scar areas of Boswarlos scallops is ascribed to the unicellular endozoic alga which infects the scallop and causes adverse effects on the soft parts of the animal. It has been shown here that the infection sets in when the scallop is about 4-6 yrs old.

When growth rates from different areas are compared it is seen that the difference in growth rates is even more pronounced. Although the

largest specimen ever recorded measured 208 mm in height (Norton, 1931) examination of shells from the Digby area would suggest that the L_∞ value (190.1 mm) computed from the data of Stevenson and Dickie (1954) is unrealistic and is in all likelihood not related to the actual maximum size that would be expected from sampling the population. Omitting the L_∞ value derived from Stevenson and Dickie's data, a general trend may be seen in L_∞ and K values with latitude. Scallops from the more northern areas have larger L_∞ values; K values are, however, generally smaller. This has been found to be the case for a variety of species including the Pacific razor clam (Taylor, 1959). Taylor (1958) makes the observation that

> ". . . rapid growth is, in poikilothermic animals at least, generally incompatible with a long life-span, and conversely, that large size and a long life-span are often associated with the cooler temperature of higher latitudes".

Holt (1959) suggests that L_∞ should theoretically decrease with increasing temperature, and that fish which approach their L_∞ rapidly, tend to have shorter lives. The present study also shows a negative correlation between K and L_∞ and higher L_∞ values are found in the more northern latitudes. There is also a relationship between longevity (as measured by the maximum age recorded) and L_∞; scallops over X^+ are fairly common in Port au Port Bay. Admittedly, however, the data are limited and the full range of the species is not covered in the present investigation. The problem is further complicated in the unique shallow-water environment where high summer

temperatures can frequently become limiting to growth. Factors other than temperature may also influence the growth rate of scallops. One such factor has been discussed already.

Natural mortality

The estimated natural mortality rate is relatively high for the population of scallops on the Boswarlos bed. Dickie (1955) calculated an average natural mortality rate for fished scallop stocks in the Digby area of the Bay of Fundy to be of the order of 10% in 1950 and considered this to be near the annual maximum. Merrill and Posgay (1964) similarly concluded that the average instantaneous natural mortality rate of scallop stocks of Georges Bank during 1958-60 was about 0.10. In his calculations for the Digby stocks Dickie used the results of some unpublished tank experiments which gave an average time of 100 days required for separation of cluckers larger than 96 mm. Merrill and Posgay extended Dickie's method and concluded that cluckers persisted for varying periods of time which was determined mainly by the environment. Using three interrelated methods they estimated the average time for clucker separation to be about 33 weeks after the death of the scallop.

In the present study an average value of 70 days to clucker separation for all ages was used in the computation for the natural mortality rate. This is substantially faster than figures reported by Dickie and Merrill and Posgay. The high rate of separation is probably due to a combination of both high temperatures and frequent mechanical disturbances. Gunter, Dawson and Demoran (1957, cited by Merrill and Posgay), working on the oyster concluded that the rate of fouling is strongly dependent upon

temperature. It seems reasonable to assume that a similar situation exists in scallop shells.

It is suggested that the high natural mortality rate calculated for the Boswarlos bed may, at least in part, be due to the relatively high rate of algal infection in these scallops. Unfortunately it has not been possible to calculate comparable figures for the West Bay and Fox Island River beds. Other causes of natural mortality in scallops have been reviewed by Medcof and Bourne (1962) and Dickie and Medcof (1963). Among those suggested, changes in water temperature may be especially important in these shallow-water inhabitants. Dickie (1958) suggests that sudden increases or decreases in temperature may debilitate scallops and render them more susceptible to predators. Exposure to lethally high water temperatures is not altogether excluded in the shallow-water scallop stocks of Port au Port Bay.

Reproduction

Hermaphroditism

The incidence of hermaphroditism in Port au Port scallops (1.3%) is greater than the reported incidence of this condition on Georges Bank by Merrill and Burch (1960) where only 2 were reported from about 3000 gonads examined. The hermaphrodites described by them had male and female parts located in different regions of the gonad. The ovary was situated near the proximal end close to the adductor muscle and the testis distal to it. The line of demarcation was irregular, follicles of one cell occurring within the tissues of the other. The hermaphrodites observed in the present

study were in a sense less 'complete' and consisted largely of patches of male tissue embedded in a predominantly ovarian matrix.

The giant scallop is an exception to the general rule that members of the family Pectinidae are hermaphroditic (Coe, 1945). It has been suggested that these hermaphrodites are due to occasional deviations in the developmental processes which result in the failure of the sex-differentiating mechanism. This results in various amounts of male and female follicles being produced and the scallops are referred to as accidental functional ambisexuals (Coe, 1942).

Breeding cycle

The determination of the spawning period is an important pre-requisite to understanding the biology of the species.

The population of scallops in Port au Port Bay shows a protracted spawning period modified to include two or more seasonal peaks of activity. The spawning period and its duration appear to vary from year to year.

Mason (1957) successfully correlated the breeding cycle of *Pecten maximus* which has two main spawnings each year with the observation that the size frequency of the first growth band had a bimodal distribution. The same plot for giant scallops in Port au Port Bay shows a very similar distribution.

The occurrence of the two spawnings in the shallow-water population of Port au Port Bay is correlated with two modes in the first year's growth on the shell. The curves for the three beds investigated are skewed to the right with definite modes toward the upper end of the

distribution. The small sample sizes may in part account for the less conspicuous representation of the modes in the scallops from West Bay and Fox Island River beds. Spring- or summer-spawned individuals will have a larger first growth band while fall-spawned scallops, represented by the larger group, will have smaller growth bands. By plotting the first growth band of any particular year-class, it should be possible to estimate the relative importance of the two spawnings for that year. A unimodal curve would indicate little or no spring or summer spawning. A bimodal distribution, on the other hand, would be indicative of at least two spawnings, the relative spread and peakedness of the individual modes indicating the contributions made by each of the spawnings to the year-class.

The occurrence of two natural spawnings a year has not been previously reported in the giant scallop although it was suggested as a possibility by Welch (1950) who stated that scallops may spawn in spring for some undetermined reason. Squires (MS, 1958) reported that the maturity of scallops throughout Port au Port Bay was well advanced in June (13th to 18th) and that they were probably spawning. Posgay (1950) found that the giant scallop may be induced to spawn by increasing temperature. Other pectinid species including *Aequipecten irradians* (Belding, 1910; Gutsell, 1930), and *Pecten latiauritus* (Coe, 1945) have also been shown to demonstrate this phenomenon. The occurrence of two spawnings in the giant scallop would indicate that in these waters the gonads become mature at different rates and that spawning is a protracted phenomenon rather than a sudden release of gametes as was described for a population of scallops on Georges Bank (Posgay and Norman, 1958). They observed that about 92% of

the scallops discharged their gametes within the relatively short span of 3-4 days. The results of the present investigation contradict the observation of Posgay and Norman and support the observations of several other workers who have assigned the mollusc an extended spawning season. It is not known if pressure changes accompanying hauls from great depths may have caused the scallops to release the free gametes. This is suggested as a possibility and may partly account for their observations. It would, however, be difficult to disprove or test the validity of their findings.

Giese (1959) discussed the environmental relationships to the annual reproductive cycle of marine invertebrates. It is difficult to determine all of the environmental factors controlling spawning in the giant scallop. Posgay (1953) believes that it may be associated with autumnal chilling of the water. Dickie (1953) suggested that it could be related to the tidal cycle. Although the major spawning in both years coincided with decreasing temperatures following the summer maxima, the occurrence of spring or summer spawning would indicate that falling temperature alone is not instrumental in initiating the spawning process. It appears more likely, depending on the state of temperature acclimation, that both temperature elevation or depression may play a part in initiating spawning. It is possible that once maturation products are within the follicles any favourable external stimulus would cause the scallop to spawn. This does not, however, explain why all the gonad products are not shed during the initial spawning in early summer. If the extent and rapidity of spawning is to some extent a gauge of the strength of the supposed stimulus that

induces spawning, then it is reasonable to assume that the strength of the stimulus varies within any one breeding season and from year to year. It is suggested that the strength of the stimulus varies with the state of thermal acclimation and that this regulates the extent of spawning observed. Dickie (1958) found that scallops rapidly acclimate to increased temperatures. This may account for the cessation of spawning after the initial outburst in early summer. After the first spawning the scallop quickly adapts to rising temperatures and further rise in temperature does not elicit a spawning response. In the fall, however, temperature decreases faster than the scallop's rate of acclimation to cold and this may provide a stronger stimulus that results in the complete extrusion of reproductive elements. In the giant scallop loss of the state of acclimation to high temperature is very slow requiring over 40 days in experimental tanks and perhaps as long as 3 months in nature (Dickie, 1958).

There is also some indication of a relation between wave action and onshore winds and the onset of spawning. In both 1966 and 1967 spawning coincided with periods of strong onshore winds and rough seas. Spawning may therefore be initiated by prolonged exposure to physical shocks.

Salinity does not vary widely in the bay (Squires, pers. comm. 1967) and it is doubtful if it controls gametogenesis or spawning.

No attempt has been made to investigate the possible existence of periodicity correlated with tidal sequence or lunar cycle. Tidal and lunar periodicity in reproductive activity has been suggested in *Pecten opercularis* near Plymouth on the south coast of England (Amirthalingam,

1928). Tang (1941) has proposed a lunar periodicity in *Pecten maximus* at Port Erin, Isle of Man. Several other instances of relationship between the moon and periodicity in the breeding of marine animals are discussed by Korringa (1947). In Port au Port Bay where the tidal amplitude is small, we may expect tides to be of little importance in determining the periodicity in reproductive activities. Reproductive periodicity in these shallow-water scallops may well be influenced by moonlight rhythm.

It is well known that the early larval stages of several species of lamellibranch molluscs are virtually identical. As far as the author is aware the pelagic larval and post-larval stages of the giant scallop have not been described. Efforts to rear giant scallops beyond the trochophore stage have so far failed. Attempts to procure young pelagic stages during the present investigation were not altogether successful. Although what is thought to be the prodissoconch stage of the giant scallop was obtained, its positive identification still awaits confirmation. If the tentative identification is accepted then this together with the relative abundance of juvenile scallops in late October would suggest that the giant scallop larva settles in about 40-50 days after hatching. Settlement may be prolonged or delayed depending on exogenous factors such as availability of food and temperature.

Unicellular algal symbiosis

The term 'symbiosis' is used here in the original broad sense of the word as defined by De Bary (1879) meaning living together ("die Erscheinung des Zusammenlebens ungleichnamiger Organismen"). Symbiotic

unicellular algae have been described from a variety of invertebrate hosts. Some of the more recent reviews of algal symbiosis include Caullery (1952), Buchner (1953, English translation 1965), Yonge (1957, 1966), Zahl and McLaughlin (1959), Droop (1963) and McLaughlin and Zahl (1966). Algal partners have been reported only from three classes of algae: Cyanophyceae, Chlorophyceae and Dinophyceae. They are often labelled as Cyanellae (Pascher, 1929a), Zoochlorellae or Zooxanthellae (Brandt, 1883a). In current terminology their meanings are largely colouristic and no precise taxonomic meaning is attached to them (McLaughlin and Zahl, 1966). As far as is known zoochlorellae have not been previously reported as endozoic algae in marine molluscs. In general zoochlorellae are usually associated with the fresh-water environment. The green alga in the marine turbellarian *Convoluta roscoffensis* and the marine hydroid *Myrionema amboinense* are exceptions, the latter harbouring either chlorellae or xanthellae depending on its geographical location (Fraser, 1931). This peculiar instance of symbiosis between the unicellular alga of somewhat uncertain identity and the giant scallop, *P. magellanicus*, so far as the author is aware, is the first reported instance of endozoic alga in the family Pectinidae.

As early as 1946, Wiborg described the occurrence of a small globular green flagellate in shallow-water populations of the Norwegian horse-mussel, *Modiolus modiolus* L. (Family Mytilidae). He thought that the organism is the same as the one responsible for the green colouration of the mantle and gill tissues of some oysters (Family Ostreidae). Mitchell and Barney (1917) and Medcof (1945) working on the American oyster, *Crassostrea virginica*, and Kerswill (1946) working on three other pelecypod

molluscs (soft-shelled clam, *Mya arenaria*; blue-mussel, *Mytilus edulis* and the ribbed mussel, *Modiolus demissus*) have attributed the green discolouration in these molluscs to the absorption of a pigment marenin through the ingestion of the marine diatom, *Navicula ostrearia*. Similarly Ranson (1927) reported *Nitzchia ostrearia* to be responsible for greening in oysters. (At the time of writing it has not been possible to determine if the two species are synonyms.) A green discolouration of the mantle and gills of oysters may also be caused by the accumulation of copper (Lankester, 1886).

Rowell (MS, 1967) reported a green ovoid microflagellate alga in the gills and mantle tissue of the horse-mussel, *Modiolus modiolus* L., from Sandy Point, New Brunswick, Canada. He did not identify the organism but points out that the 'algal infestation' is a phenomenon of shallow-water populations of the horse-mussel.

The green colouration in the horse-mussel observed by Wiborg and Rowell, as in the giant scallop, is due to the presence within the tissues of an infecting organism rather than a colouration acquired through the deposition of metabolic pigments. The more salient features of the three associations are listed in Table 33. Rowell, on the basis of the size and shape of the flagellate, suggests that the alga described by Wiborg is different from the one found by him in populations of intertidal horse-mussels on the Atlantic coast. In the absence of a positive diagnosis it is impossible to say if the infecting organism in the scallop is similar or even related to the microflagellate reported by Rowell.

Table 33. Comparison of the incidence of unicellular green alga(e) in *Modiolus modiolus* and *Placopecten magellanicus*.

Investigator	Host organism	Description	Size	Infection site
Wiborg (1944)	*Modiolus modiolus*	small, globular flagellate	about 12μ	siphon and mantle edges
Rowell (MS, 1967)	" "	green ovoid microflagellate	4.6μ length 3.1μ width	gills and mantle
Naidu (this paper)	*Placopecten magellanicus*	bright green, round to oval unicellular alga	1.5-5.0μ in diameter	right and left mantle lobes, distal end of gonad and bases of the adductor muscle

It is initially surprising to find that the symbiotic relationship has not been reported or recognized previously in the giant scallop, much work having been done on this commercially important mollusc. On closer examination it has been shown here that the phenomenon is restricted to shallow-water populations of *P. magellanicus* inhabiting the more northerly latitudes. Although the giant scallop has been commercially exploited in Port au Port Bay by both Newfoundland and Nova Scotia fishermen there has

been no study made on the biology of the species there. The shallow-water habitat in the Newfoundland area appears to be responsible for a number of peculiarities observed in the population there, of which the unique symbiotic association with the photosynthetic alga is only one.

Although the initial stages of the infection have not been thoroughly investigated, some indication of the possible origin of the association may be seen in the observation that the occurrence of the algal symbiont is associated with shell deformities. Exactly how the scallops become infected with the alga is unknown. Available evidence indicates that the alga becomes lodged within the mantle tissue of the scallop through the surface epithelium rather than as a result of ingestion. From my observations a sequence of phases may be recognized through which the association probably develops. The convenient phases proposed by Cheng (1967) are adopted here.

The period of initial host-symbiont contact appears to be associated with shell damage or shell growth impairment at some point along the shell margin. Several factors may disrupt the normal pattern of shell growth. Foremost amongst these is the damage caused as a result of severe shocks. Damage through the dragging activity of the fishing fleet could be important where the scallops are exploited by the fishery (Medcof and Bourne, 1964). There is, however, no commercial fishery on the Boswarlos bed. These shallow-water populations are, however, frequently affected by storms, when bombardment by sand particles and small pebbles can cause mantle retraction. Merrill (1960) suggests that foreign matter lodged between the mantle and the shell may cause layering in the valves of the scallop.

Normal shell growth may also be impaired by epifaunal associations on the surface of the shell, especially when foreign organisms settle too close to the shell margin. *Lithothamnia* sp., for example, may overgrow the lip of the shell and interfere with the mantle, causing shell distortion.

Whatever the cause the scallop acquires the algal symbiont through the mantle. As in other lamellibranchs the mantle tissue of the scallop is the site of contact with the external environment. It is suggested that the alga becomes associated with the scallop when the animal for some reason or other becomes temporarily enfeebled. This observation strongly suggests that the initial phase may therefore be largely accidental and random. Several other factors including the selectivity of the symbiont, the host's feeding mechanisms, or even a chemotaxic attraction, are possible and cannot be dismissed. Host secreted attractants may aid in the initial contact process. The mantle fluid itself may be a rich source of nutrients to the alga. The mantle fluid of the oyster, for example, is known to be rich in proteins and amino-acids, the amount secreted being influenced by the physiological state of the animal (Galtsoff, 1964).

The second phase involves the colonization of the molluscan host by the algal symbiont. The infection spreads from the point of initial contact along the mantle edge while at the same time spreading farther away from the shell margin into uninfected tissues. It is possible that both feeding and respiratory currents aid in the process of colonization within the scallop.

The exact mechanism of escape and transmission of the symbiont from the host remains unresolved. It is probable that a free swimming stage

exists. The pre-symbiotic stages of the alga have not been collected in the plankton. The association, however, is not hereditary but commences anew in each generation. It is terminated with the death of the host. The association is thus a facultative one, that is, each of the two participating organisms is capable of autonomous existence. This is indeed emphasized by the presence of both uninfected scallops and the occurrence of free algal colonies on the inner shell margins of heavily infected scallops.

The presence of reproductive phases within the scallop is significant, for it implies that the alga has overcome the internal defence mechanisms of the scallop and is successfully established within the molluscan host. Cheng (1967) defines successful establishment of a symbiont as "the ability of the symbiont to become located at a suitable site and to succeed its normal physiological and reproductive processes".

Although a marked seasonality in the occurrence of the unicellular alga within the molluscan host has not been convincingly demonstrated in the present study there is evidence to suggest that there is perhaps a massive reinfection of potential hosts in early spring when the alga is presumably abundant with fewer new infections as the summer proceeds. Removal by death of heavily infected senile or moribund animals may account for some of the observed decrease in the reported monthly percentages.

The availability of light within the scallop appears to be important. The mantle lobes are the obvious loci of the alga for exposure to maximum light. Some light must, however, get into the other potential areas of infection. When the left or upper valve of a scallop is held against

a light source areas of light transmission are readily seen. Both the shell margin adjacent to the mantle edge and the adductor muscle scar transmit light more readily than the other parts of the valve. It is precisely in these regions that the algal colonies are especially abundant. Some diffuse light may account for the scattered colonies on the gonad. The presence of algal colonies on the gonads and bases of the adductor muscle would seem to indicate that only a small amount of light energy is required for photosynthesis.

Sex does not appear to exercise an influence on the resistance or receptivity of the algal symbiont.

The functional significance of algal symbioses among marine invertebrates has been reviewed by Yonge (1944, 1957), Fritsch (1952), Droop (1963) and McLaughlin and Zahl (1966). The nature of the relationship varies widely in different associations. The full biological significance of the relationship between the alga and the giant scallop is at present obscure. Further work will undoubtedly be required to ascertain the exact nature of the association. From a purely speculative viewpoint it is possible that the oxygen produced by the alga during periods of active photosynthesis can be used by the mollusc. Carbon dioxide produced by the mollusc may in turn be taken up by the alga during carbon fixation. Organic substrates may also be removed by the plant. The nitrogen and phosphorus wastes of the animal should be of special importance to the alga that could be living in an environment frequently exhausted or scarce of these nutrients (Droop, 1963). Such a condition, when essential nutrients become temporarily exhausted, may be provided during early spring when primary

production is at a maximum. The alga in turn can provide some of the carbohydrate requirements of the animal as well as other nutrients through their death. The uptake of metabolic products of carbohydrate nature by the scallop during the vigorous growth of the alga is not altogether excluded. The nutritional requirements of the alga are at present unknown.

Since the alga is not only in contact with the host tissue but is often in intimate contact within the tissues of the host and since it has an overall adverse effect on the scallop when present in large numbers, it appears reasonable to assign the alga the status of a parasite.

Economic importance

In North America only the large posterior adductor muscle is considered edible today. The 'eye' or 'heart' as it is so often called by fishermen is white, glossy and plump in the healthy scallop. The meats of infected scallops are often darker and stringy and may no longer be marketable. The mantle and gonad are generally discarded at the present time and the presence of the alga within them is important only in so far as it affects the condition of the adductor muscle.

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